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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 82, NO. 5, PP. 325–338 SEPTEMBER, 1955

EMBRYOGENY IN THE LIMA BEAN

CLARENCE STERLING

Two previous papers (Sterling 1954, 1955) have described the ontogeny of seed coat, nucellus, and endosperm in lima bean (*Phaseolus lunatus* L.). To complete this series on seed development, the present study deals with various aspects of embryo growth and differentiation.

Although virtually no attention has been devoted to the embryogeny of *P. lunatus*, certain phases of structure and development in the embryos of legumes have been intensively explored. Sequences of the early embryonic divisions have been worked out for various Leguminosae by Souéges (1927, 1946, 1949, 1950), Scrobichewsky (1885), Guignard (1881), Rau (1951), Cooper (1933), and others. Specific attention has been given to this stage in *P. vulgaris* by Brown (1917), Scrobichewsky (1885), Souéges (1950) and Weinstein (1926) and in *P. multiflorus* by Guignard (1881).

However, histogenesis during the later growth of the embryo is less well known in this family. Bordás (1932) has presented an account of this phase of embryo development in *Cicer;* Guignard (1881) briefly considered histogenesis in various species of legumes; Hegelmaier (1880) evaluated development in the lupine embryo from the standpoint of the histogen concept, as did Neumann (1939) in both *Lupinus* and *Mimosa;* and Reeve (1948) has described late embryogeny in *Pisum*. Tiegs (1912) was concerned principally with development of the root apical meristems in the embryos of *Pisum* and *Vicia*. No studies have been made on this stage in *Phaseolus* embryogeny.

Anatomical studies of the mature embryo have been reported for many legumes, including *Phaseolus*. Besides the detailed histological accounts of various genera by Harz (1885) and Pammel (1899), Beck (1878) has described carefully the embryo of *Vicia*, Bordás (1932) that of *Cicer*, Godfrin (1884) *Arachis*, Newman (1934) *Acacia*, and Schmidt (1902) various Loteae. In the genus *Phaseolus*, histological details have been given for *P. vulgaris* by Doutt (1932), Godfrin (1884), and Kater (1927), and for *P. multiflorus* by Sachs (1859).

Materials and methods. Details concerning the materials and the histological techniques have been presented in the first paper of this series (Sterling 1954). That paper also defines the specific terminology of planes and directions for the bean ovule.

Proembryo development. Because of the great rapidity of events in early embryogeny, union of the male gamete with the egg nucleus was found in only one instance in the Evergreen beans and not at all in the

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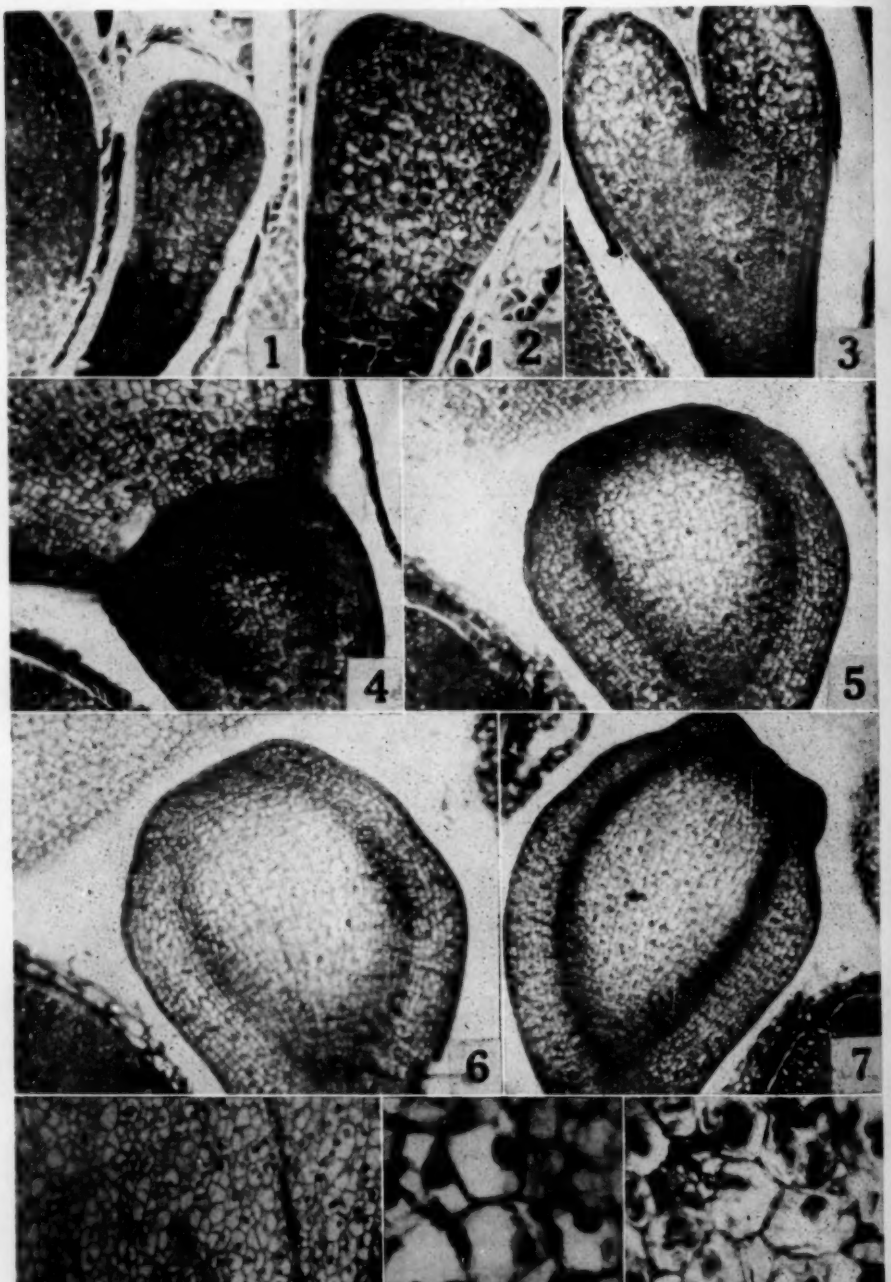
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Henderson Bush variety. During the two days following fertilization, the zygote divides by a transverse[1] wall to form two cells. The anterior (or basal) cell then divides in turn by a transverse wall while the posterior (or apical) cell may divide either by a transverse wall or one that is obliquely vertical. Thus four cells are formed in the young embryo while the endosperm is still free nuclear (*ca.* 16 nuclei) and parietal.

Succeeding growth is extremely rapid. By the third day, the two basal cells have formed a suspensor four cells long and two cells wide. The suspensor is surmounted by a globular mass of 16–32 cells derived from the two apical cells. At the apex of this embryo there may be found occasionally a more or less tetrahedral apical cell. Within two more days, each of the suspensor cells again divides by a transverse wall, elongating greatly in the process. Simultaneously, the apical embryonic group grows to approximately 64 cells by transverse divisions and divisions in the median and frontal planes (fig. 1). Some periclinal divisions occur at the surface of the globular mass, but the general appearance suggests the organization of a protoderm. At this time, cell walls are formed about the embryo in the endosperm tissue.

Cotyledon initiation. At about one week after fertilization, when the embryonic group of cells is approximately 250 μ long (at the end of a suspensor which is about 300 μ long and composed of eight superposed tiers of cells), cotyledons are initiated. Two cotyledon primordia are produced, one on each side of the median plane of the seed in the Henderson Bush variety[2]. Periclinal divisions in the protoderm layer and below attend this emergence,

[1] Actually somewhat at an angle to the transverse plane as defined in Sterling (1954), due to ovule curvature.

[2] However, a constant feature of the Evergreen embryo is the formation of the cotyledon primordia in a plane *oblique* to the median plane. No exceptions were found to this early orientation of the cotyledon plane, which often persists to maturity.

FIGS. 1–10. Suspensor toward bottom of page in all. All figures of Henderson Bush embryos except where indicated otherwise. FIG. 1. Embryo at 4 days with establishment of protoderm. Note periclinal divisions in protoderm layer. Deep stain in suspensor cells is characteristic. ×200. FIG. 2. Late initiation of cotyledons in Evergreen embryo at 10 days. (Section is in transverse plane of ovule.) Periclinal divisions occur in surface layer and underlying tissues at regions of cotyledon emergence. ×210. FIG. 3. Elongating cotyledons of 8 day embryo in transverse plane of ovule. Procambial cells not yet distinct. ×151. FIG. 4. Expansion of embryo in median plane is marked at 10 days. Differentiation of procambial cylinder has become apparent. ×151. FIG. 5. Embryonic cortex and pith are quite distinct in smaller 13 day embryo. Note gradual raising of apical region of embryo above hypocotyledonary body. Root apical meristem beginning to become active. ×122. FIG. 6. Buttresses of future foliar primordia becoming more noticeable, also in smaller 13 day embryo. ×122. FIG. 7. Emergence of foliar primordia at 13 days in larger embryo. Note beginning of formation of small apical dome between the two primordia. ×91. FIG. 8. Portion of cotyledon of same embryo as in figure 7, showing small procambial strands and absence of starch in the parenchyma cells. ×91. FIG. 9. First obvious development of amyloplasts, with starch, in cotyledon of 17 day embryo. ×298. FIG. 10. Parenchyma cells in cotyledon of 25 day embryo, showing enlarged envelopes (at arrow) about growing starch grains. ×210.

which is preceded by the widening of the embryo in the frontal plane to form the cotyledonary buttresses (fig. 2).

In the larger seeds at one week, the cotyledons are up to 50–60 μ high, above their insertion region. The embryo apex remaining between the cotyledons is flattened in the median plane, quite narrow (5–15 μ wide) in the transverse and frontal planes (fig. 3), and inactive in appearance. In the median plane, the embryo apex is broadly convex, extending the full width of the embryo (120–140 μ).

Procambial differentiation. When the cotyledons are about 100–200 μ high, there is still no evident procambium in these nor in the main body of the embryo (fig. 3). At this time (8–10 days), the cells at the apices of the cotyledons begin to enlarge and acquire large vacuoles while the cells at the bases remain smaller and more actively meristematic (fig. 4).

In the embryo body, however, parenchymatous differentiation of pith and cortex begins to block out the procambial cylinder of the hypocotyl-radicle axis (fig. 4). On the lateral flanks, a cortical parenchyma develops in the lower portion of the still more or less globular embryo mass, and in the center, near the apical region, an obconical pith parenchyma region is formed. Thus a procambial region, in the shape of a cup, is set off.

At first, the procambial cells at this stage differ from their parenchymatous neighbors only in their deeper stainability, later also by their smaller size and smaller vacuoles. They may be found in the lower region of cotyledons which are about 200 μ high as well-defined, acropetally developing strands (also Reeve 1948, in *Pisum*).

Formation of the root apical meristem. As the suspensor continues development, it becomes 6 cells wide just below the embryo proper. Towards the base (micropylar end) of the suspensor, the rate of cell division decreases, and there is an increase in the amount of cell elongation. At its basal tip, the suspensor terminates in two large, much elongated cells which lie side by side.

In larger embryos collected at 10–12 days (when cotyledons may almost fill the embryo sac in larger seeds) there is evident the first sign of the organization of a root apical meristem. This is found at the level at which the obconical embryo body just begins to become wider above the suspensor. The root apical meristem becomes noticeable as a region of active transverse[3] divisions from which the longitudinal cell rows in the procambium and pith appear to diverge. Above the root apical meristem, cells in the pith and procambium experience transverse and longitudinal divisions, *i.e.*, "T" divisions (Wagner 1939 and others). Cell rows are also continuous from this meristem into the suspensor.

[3] See footnote 1. The division walls are transverse to the longitudinal axis of the embryo and almost coincide with the transverse plane of the seed.

In the cortical region and in the protoderm, the cell rows have no connection with the root apical meristem at this time. Instead, they run from the hypocotyledonary region without change into the outer suspensor, through the region which will become the root cap (fig. 5). However, this relationship is subsequently altered.

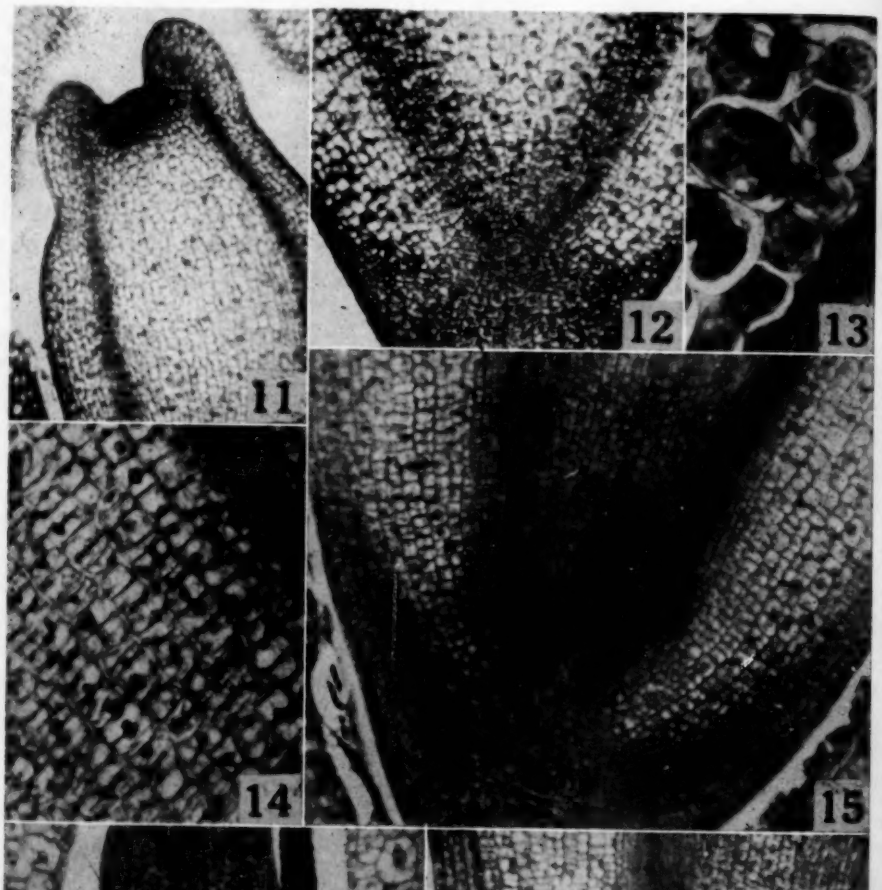
Epicotyl development. As the age of the embryo approaches two weeks, the embryo apex begins to enlarge in both the median and frontal planes (fig. 5). At ten days, its frontal diameter attains to 20–30 μ and its median diameter to 200–220 μ. Fewer and fewer periclinal divisions are to be found in the surface layer of this apex.

On the thirteenth day, the median diameter of the embryo apex reaches 260 μ. The embryonic body extends about 320 μ from the suspensor to the free apex. At this time, the cotyledons may be 1500–1800 μ long, with marked growth throughout: active divisions in the basal meristem; frequent mitoses in the vacuolating parenchyma in the body of the cotyledons; and a rapidly extending, anastomosing network of thin procambial strands (fig. 8).

Whether the whole rounded apex of the embryo is properly to be called shoot apex is questionable. The emergence of the first two foliar primordia, which takes place in the larger seeds at two weeks, does not involve the broad shoulders of the embryo apex. Instead, that portion of the apex lying immediately between the insertion regions of the cotyledons begins to widen markedly in the median plane. Periclinal divisions in subsurface cells in this region raise a broadly rectangular mass (fig. 6). Activity at the two sides of this mass, in the median plane of the seed (constituting two foliar buttresses), raises two opposed leaf primordia (fig. 7) above the level of the embryo apex, the included portion of which is now indubitably a "shoot apex." Since no further periclinal divisions are to be found in the surface layer of the latter, that layer may accordingly be designated as a "tunica." Before the appearance of the primordia, acropetally developing procambial tissue is evident in the foliar buttresses (fig. 6).

Overall histogenetic development of embryo at two weeks. When the opposed, young leaf primordia are 60–90 μ high, the shoot apex between them is more or less flat (about 70 μ wide in the median plane). A mantle of "eumeristem" (Kaplan 1937, Sterling 1945) over the shoot apex is continuous with the procambial cylinder below and with the procambial strands of the newly emergent foliar primordia (fig. 7). There is no discontinuity in the organization and development of the procambial tissue (fig. 11).

Elongation of the embryo body is occurring constantly by means of cell elongation in all tissues (the cells of the procambial tissue are now noticeably much longer than surrounding cells) and by rib-meristem activity in embryonic pith and cortex. Occasionally transverse divisions occur in the procambium but less noticeably so than in the parenchymatous neighbors. At its widest diameter, the pith region of the hypocotyl is 20–23 cell rows across,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and there are 8–9 rows of cells in the cortex between the procambium and the protoderm. Longitudinal divisions occurring in cortex and pith serve to slowly increase the numbers of cell rows in these tissues and hence the diameters of the tissues.

At this time, there is no connection between the cell rows of the cortex and the root apical meristem, the former being continuous with rows of cells which converge laterally below that meristem in the root cap region (fig. 7). However, the longitudinal cell rows of pith, procambium and central region of the suspensor (not a "column" here) show clear derivation from the root apical meristem (fig. 12).

In some of the larger seeds at 14 days, the cells of the root apical meristem are larger and less active than their derivatives (*cf.* the "focal" area similarly located in development of the *Taxus* embryo, Sterling 1949a). About this focal zone of the meristem, the derivative cells experience active divisions, in which the new walls are arranged concentrically about the focal zone. In this spherical area, most frequent mitoses are to be found immediately above and below the focal zone (fig. 12). The new cell walls in the lateral regions tend to disrupt the continuity of the cortical cell rows.

Third week of embryo development. During the next week of growth, the remainder of the embryonic primary tissues are formed. In the cotyledons, very extensive procambial networks are produced. The parenchyma cells here acquire starch grains about 17 days after fertilization. On their first appearance (fig. 9), the grains are too small to give polarization crosses, but within a few days they become much larger and definitely birefringent. The starch grains are usually simple and may be up to 20 μ long at this time; each appears to be individually encapsulated in a mass of material of notable thickness (fig. 10).

At the shoot apex, which is large and convex, the bases of the two enlarging foliar primordia extend about the apex and are in contact with each other. At the points of their union occur enlarged proliferations, which will form the morphologically fused stipules during germination (fig. 16). However, at this time and up to maturity, these proliferations merely constitute

FIGS. 11–17. Suspensor toward bottom of page in all. All figures of Henderson Bush embryos. FIG. 11. Large embryo at 13 days, with enlarging foliar primordia. Note acropetally developing procambial strands. ×91. FIG. 12. Root apical meristem of large 13 day embryo. ×151. FIG. 13. Portion of cotyledon of near mature embryo at 34 days. Starch grains occupy most of protoplast in parenchyma cells adjacent to procambial strand at lower right. ×210. FIG. 14. Portion of pith of hypocotyl in 28 day embryo. Rib meristem activity is proceeding via many mitoses. Part of procambial cylinder at upper right. Root apical meristem is situated toward lower right here. × 210. FIG. 15. Root apical meristem and derivative regions in 22 day embryo. ×170. FIG. 16. Shoot apex in epicotyl of 22 day embryo—cut in transverse plane of ovule. Stipule primordia evident on lower shoulders of the apex, with portions of the first foliar primordia sectioned above the apex. Cotyledons at sides of figure, with shell zones in their axils. ×122. FIG. 17. Root apical meristem at 34 days. Portion of suspensor is attached. ×122.

two mounds of tissue on either side of the embryo, in the frontal plane. In the axils of the cotyledons may be seen "shell zones" (concentric arcs of cells), as described by Schmidt (1924); however, no bud primordia are formed in the embryonic stage.

The basal derivatives of the root apical meristem toward the suspensor are displaced laterally due to vertical divisions, followed by isodiametric cell enlargement. The displacement of these cells and the concentric divisions

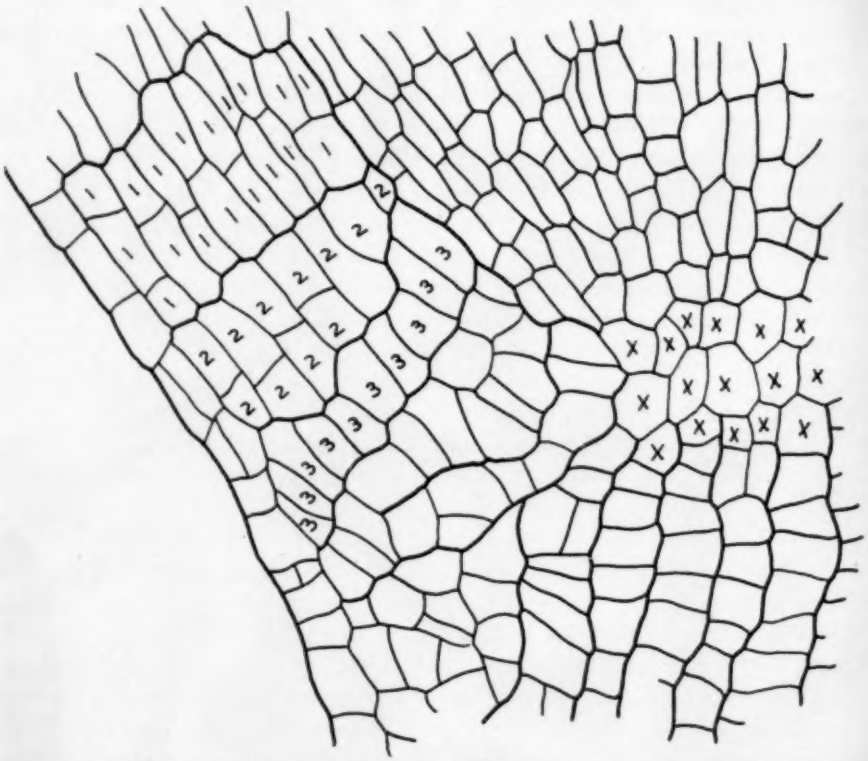

FIG. 18. Line drawing of longisection of Henderson Bush embryo (15 days) in region of root apical meristem. Cells of primordial meristem indicated by "x". Related groups of sister cells in cortex are numbered alike. Note discontinuities along boundaries of major groups, showing that cells across the boundary in any particular vertical row are not sister cells.

which continue, together produce a cell conformation in which the cell rows of the cortex appear to be continuous with the concentric layers of root cap cells below and about the root apical meristem (figs. 15 & 18). As the rapid elongation of the hypocotyl-radicle axis proceeds, the root apical meristem is thrust past the lateral derivatives which lie near the protoderm[4], and those

[4] The protoderm is still continuous over the root cap.

derivatives are passively elongated. Thus the root cap appears to be giving rise to the cortex, particularly because the now more or less vertically directed cells (which arch from below) experience transverse divisions in the same fashion as the other cortical cells. This organization persists during further development (fig. 17).

Although the lengths of the suspensor and of the root cap region remain relatively constant, there is a tremendous elongation of the embryo axis. This elongation is attended by intensive rib-meristem activity in the pith and cortex regions of that axis. Coincidentally, the diameter of these regions also increases to such an extent that there are now 16 longitudinal cell rows along a radius in the cortex and 25 cell rows comprising the pith diameter. The procambial cylinder is 8–10 cells wide.

Maturation and vascular differentiation. Within the next three weeks, as the size of all organs of the embryo increases by cell division and eventual enlargement, certain cells on the medullary side of the procambial cylinder become set off from their neighbors. These cells are superposed in uniseriate rows and occur in groups at four symmetrical positions in the radicular procambial cylinder (tetrarch organization). The cells in question enlarge, becoming quite wide, and their cytoplasm stains less intensely and tends to shrink away from the cell wall.

At this pre-germination stage, these elements cannot be definitely assigned to a particular vascular tissue. Perhaps in accordance with the many observations of the development of phloem as the first indication of differentiated vascular elements in the root (Esau 1943, and others), these may be presumptive sieve elements. The elements occur throughout the hypocotyl, as well, and can be followed to within 80 μ of the root apical meristem in the near-mature embryo. No other indications of vascular differentiation could be found in the embryo as late as 45 days after fertilization. (In the embryo of *P. multiflorus,* Beck (1878) has recorded the occasional presence of xylem vessels in the cotyledons. According to Sachs (1859) however, these elements are lacking.)

Within the hypocotyl, the pith diameter increases to 33 cell rows, and its cells enlarge transversely to the long axis of the pith, in some cases acquiring a near-tabular shape (fig. 14). Rib-meristem activity ceases, and small starch grains begin to form in the cells of the pith. Starch also is produced in the cells of the root cap and the cortex, although less abundantly in the latter. Starch grains do not occur in the procambium or in the epidermal cells anywhere in the embryo.

In the enlarging simple starch grains of the cotyledons, the hila of Evergreen beans remain punctiform for a long time. However, in Henderson Bush beans, the formerly punctate hila became greatly elongated cracks in the axis of the major diameter of the grains (fig. 13). These cotyledonary grains ultimately attain a length of 30–40 μ. Not infrequently compound

groups of smaller grains (with as many as 6 moieties) may be found among the large simple grains of the parenchyma cells.

The epidermal cells of the cotyledons are tabular in cross-section and relatively uniform. No indication of stoma formation or guard cell differentiation is evident. Although stomata have been described in *Phaseolus* by Tognini (1897), Schleiden and Vogel (1839) and Doutt (1932), their presence has been denied by Godfrin (1884), Gris (1864), Kater (1927), and Sachs (1859). Careful examination of the cell walls in the cotyledonary parenchyma does not confirm the picture given by Frear (1883). The cell walls are quite thin and covered with primary pit fields. There is no thick lamella of primary wall overlying the middle lamella. Frear's interpretation was apparently founded on sections which passed through portions of walls which were more or less parallel to the plane of section.

Further developments are regressive, leading to the incipient shrinkage and hardening of the embryo after the 45th day.

Discussion. Because of the extensive studies of very early embryogeny in related species and the essential correspondence of early lima bean development with that of other legumes, it is unnecessary to discuss this phase here. No distinct anatomical developments could be correlated with the time of optimum organoleptic quality of the fresh bean.

Primary interest attaches to the phases of development in which the procambium is blocked out and in which the root apical meristem is organized and develops. With the techniques used in this investigation, it is of interest to note that the first sign of procambium formation is not apparent until the primordia of the cotyledons are fairly well grown. This contrasts with the early blocking out of that tissue (prior to cotyledon emergence) in the embryos of *Taxus* (Sterling 1949a) and *Phlox* (Miller & Wetmore 1945). The earliest indication of the procambial cylinder in the hypocotyl axis is due principally to a change in stainability of cells in the regions of future cortex and pith. The cells of the early procambium are otherwise undifferentiated from their neighbors. No indication is found of basipetal differentiation of procambial tissue into the hypocotyl from the cotyledonary node.

The formation of the root apical meristem is attendant on the widening of the suprasuspensory region of the embryo. The larger, somewhat more vacuolate cells of this meristem divide less frequently than their concentrically produced derivatives. The initial zone may therefore properly be considered as a "focal zone" in the sense used earlier (Sterling 1949a). From this focal zone of initials are produced radiating rows of derivative cells, "eumeristem," distally toward the suspensor-root cap region, laterally, and proximally toward the hypocotyl body.

Evidence for histogenic derivation (Tiegs 1912, and others) of the various tissues of the radicle from various layers or specific cells of the initial zone is not to be found in the lima bean embryo. It is obvious from figure 18,

first of all, that the mechanism of the divisional activity is not, as indicated by Clowes (1950), a point to point derivation of cortical cell lineages from specific cellular units in the meristem. Rather, radial rows of a precortical primary meristem are produced by the initial zone, the cells of these rows then becoming active as initials of a rib meristem, as they are displaced by new rows. Evidence of this interpretation of the mechanism of growth of the root apical meristem is indicated in other plants by the figures of Clowes (1950): Pl. 3b; Schade and Guttenberg (1951): fig. 7; Sterling (1949b): fig. 17; Nast (1941): Pl. V, fig. 18; Pl. VII, fig. 24; and Yarbrough (1949): fig. 10. Additionally, the concept of an inverted cup of histogen initials does not fit well with the distribution of growth in the enlarging radicle of the lima bean embryo.

A second point of contradiction to histogenic derivation of radicle tissues is evident in figures 12, 15, and 17, in which it may be seen that the various tissues differentiate irrespective of cell boundaries. Vacuolarization and cell enlargement in the future cortex transgress the lines of cell boundaries, so that no distinct cellular limit may be drawn between cortex and the proximal region of the root cap. A distinct epidermal histogen is lacking. Likewise no clear distinction can be made between particular cell rows unique to the cortex and to the procambium, nor is there a distinction in origin between cell rows of the procambium and those of the pith.

It is also necessary to consider the neo-classical view of the presence of an "apical cell' in the dicotyledon root apical meristem (Guttenberg 1947, Neumann 1939, & Schade & Guttenberg 1951). Theoretically, it is possible to conceive that such a cell is likely to exist where a distinct meristem layering is absent. Nevertheless, the *effective* primordial meristem (like the effective cambium) seems to be a group of cells of similar cytological aspects and properties (see also Clowes 1953, 1954). The organization of the unlayered meristem in lima bean and related plants flows naturally from the concept, as well as physical presence, of a group of cells on the boundaries of which more active derivatives produce radiating rows of cells. By subsequent differential growth activity, *i.e.*, "T" divisions (Reinke 1871, 1872; Wagner 1939; Clowes 1950, 1953, 1954), these radiating rows create the various patterns to be found in the root tip (also see Reeve 1948).

Use of the term "eumeristem" has recently been questioned by Johnson (1951). From the work of Kaplan (1937) and Buvat (1944–45, 1952), it is clear that various types of meristematic cells are cytologically non-equivalent. It appears to the author that a more heuristic prospect will follow the analysis of zonation in apical meristems based on such cytological differences than would issue from an interpretation of meristem structure on the basis of the types of derivative tissues. It seems more appropriate to regard the root apical meristem here as consisting of a less active "focal zone" which gives rise, by greater activity at its margins, to eumeristem cells. From these

eumeristem cells the various primary meristems then appear to be developed. A view point such as this will generalize similarities in meristem construction rather than emphasize dissimilarities which may obscure relationships of interest in developmental anatomy.

SUMMARY

1. Early embryogeny in *Phaseolus lunatus* closely resembles that of other members of the genus.

2. Cotyledon primordia are formed before procambial tissue becomes obvious; but when differentiation of the latter is apparent, its direction of development is acropetal.

3. A root apical meristem develops as a focal zone of less active cells surrounded by a spherical shell of more active, concentrically dividing eumeristem cells.

4. No histogenic layers are to be found in the root apical meristem or its derivatives.

5. The epicotyl consists of two opposed primary leaf primordia, in which procambial tissue develops acropetally. Stipular primordia are also present.

6. No relationship could be found between anatomical development and the stage of optimum organoleptic quality.

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MECHANICAL TRANSMISSION OF CLOVER CLUB-LEAF VIRUS TO ITS INSECT VECTOR

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In 1943 Black discovered a new leafhopper-transmitted plant virus which he named clover club-leaf virus, *Aureogenus clavifolium* Black (Black 1944). This virus has never been reported as a plant pathogen occurring in nature, although in experimental inoculations it caused a disease in crimson clover (*Trifolium incarnatum* L.) and in periwinkle (*Vinca rosea* L.). Perhaps the most interesting features of the relationship of the club-leaf virus to its insect vector *Agalliopsis novella* (Say) are transmission of the virus through the egg of infective females to their progeny (Black 1948) and multiplication of the virus in vector insects (Black 1950). At present only 5 other leafhopper-borne viruses are known to pass through eggs of vectors to the progeny. These are the viruses causing rice stunt (Fukushi 1933), wound tumor (Black 1953), potato yellow dwarf (New Jersey variety of the virus) (Black 1953), alfalfa dwarf (Grylls 1954), and a newly discovered virus (Maramorosch 1953) in western Europe (Evenhuis, personal communication; Maramorosch, unpublished data). The study of these leafhopper-transmitted plant viruses is of considerable basic importance. The ability to maintain themselves in insects places them in a special category of insect, as well as plant, viruses. In addition to these plant-pathogenic viruses, a virus of the fruitfly *Drosophila melanogaster* (L'Heritier & Teissier 1937) also was found to pass through the egg to the next generation. Only 2 of the 7 viruses transmitted through the egg to offspring, the *Drosophila* virus (L'Heritier & Hugon de Scoeux 1947) and the wound-tumor virus (Maramorosch, Brakke & Black 1949), have been transmitted mechanically to their respective insect hosts by means of injections. The club-leaf virus has never been transmitted mechanically. It could not, therefore, be studied *in vitro*, as it has not been possible to detect the virus in extracts from insects or from plants. The purpose of the present investigation was to find, if possible, a mechanical means of virus transmission from cell-free extracts of plant and insect material.

Materials and methods. The leafhoppers used in the experiments were originally obtained from stock cultures of virus-free and virus-bearing *Agalliopsis novella*, maintained by Prof. L. M. Black at the Department of Botany, University of Illinois, Urbana, Illinois. Immediately after the shipment arrived in New York, the viruliferous leafhoppers were placed on sweet clover plants (*Melilotus alba* L.) and maintained for 3 months at 25° C. in controlled temperature chambers described previously (Maramorosch 1952).

The controlled temperature was of importance because club-leaf virus is heat labile (Black 1950, Black, unpublished data), and the infectivity of the vectors might have been impaired seriously by ordinary summer greenhouse temperatures. The virus-free leafhoppers were maintained in a greenhouse insectary on either sweet clover or alfalfa plants (*Medicago sativa* L.). Crimson clover plants (*Trifolium incarnatum* L.), used for the infectivity tests, were grown from commercial seed in a mixture of sand and soil in 6 in. pots and later transplanted to 2 in. pots when the plants reached a height of approximately 1 in. These plants were caged in transparent celluloid cylinders provided with plastic screen tops for ventilation. Small cages were prepared conveniently by replacing the bottoms of commercially available cellulose nitrate containers (manufactured by the Lusteroid Container Corporation, Maplewood, N. J.) with a fine screen of Lumite, 60×60 mesh.

A specially constructed automatic microinjection apparatus was used for mechanical inoculations (Maramorosch, in press). Virus-containing solutions were obtained from insect and plant sources. When the source was viruliferous *Agalliopsis novella*, 40 adult leafhoppers were macerated at 0° C. in a commercially available 2 ml. TenBroeck tissue grinder and a few drops of a modified Ringer solution were added to make a 1:30 dilution by weight. One liter of the Ringer solution contained NaCl 9 grams, KCl 0.42 grams, $CaCl_2$ 0.06 grams, dextrose 0.5 grams, $NaHCO_3$ 0.5 grams. The suspension was centrifuged at 4000 r.p.m. for 10 min. in a coldroom at 0° C. and the supernatant fluid used for inoculations. The vial containing the inoculum was kept in a mixture of ice and water and the micropipettes were refilled after four inoculations. When the virus-containing solutions were prepared from diseased crimson clover plants, leaves were macerated with phosphate buffered sodium chloride solution instead of the modified Ringer solution. The sodium chloride solution contained NaCl 0.225 M, K_2HPO_4 0.0067 M, KH_2PO_4 0.0033 M, and had a pH of 6.9 (Brakke, Maramorosch & Black 1953). The dilution, centrifugation, and cooling of the inoculum were similar in both cases. Insects from virus-free stock, chosen for the tests, were divided at random into four equal groups of 50 individuals. One group was injected with diluted insect juices, another with diluted plant juice, and two groups were not injected and served as controls. The inoculated insects and the controls were tested in groups of 5 or less on a total of 80 crimson clover plants. After the removal of insects, all exposed plants were kept in a greenhouse and observed for 8 weeks or longer.

Experiments and results. Almost all control insects survived the first 4 weeks, after which they were transferred for 6 weeks to a second lot of plants. All clover plants of the first as well as of the second lot exposed to control insects remained healthy. Only 39 insects inoculated with insect or plant juices survived the first 4 weeks. Afterwards these insects were tested

individually on young crimson clover plants. Of 22 insects inoculated with material of insect origin, 6 proved infective. Of 17 leafhoppers inoculated with plant juice, 3 transferred the virus. The incubation period of the virus in inoculated insects was longer than 4 weeks but no attempt was made to establish the exact length of this period. The incubation period in clover plants varied from 5 to 8 weeks.

In addition to tests with insects inoculated mechanically, a routine test of the virus-carrying *Agalliopsis novella* was made to ascertain whether these insects still carried the virus and also whether infection would be produced under the conditions of the experiment. By the end of September 1953, 120 insects from viruliferous stock were caged for 10 days in groups of 5 insects on 24 crimson clover plants. Within 3 months 17 of the 24 plants showed club leaf. This result indicated that the insects maintained a high degree of infectivity, probably as a result of their maintenance at the controlled temperature of 25° C. during the summer.

Discussion. In his experiments Black (1950) demonstrated beyond doubt that club-leaf virus multiplies in its insect vector. Mechanical transmission of this virus, as here described, now provides a technique whereby this virus can be detected in extracts from viruliferous insects and from diseased plants. It seems that virus inoculated mechanically into a vector leafhopper is distributed in the blood from the abdominal cavity to tissues where it can multiply. As pointed out before in connection with other leafhopper-transmitted viruses, the insect host obviously is more susceptible than the plant host to infection by mechanical inoculation. The club-leaf virus has not been transmitted to plants by needle inoculation or by rubbing, probably because of its low concentration in extracts from plants. Neither was virus obtained from animal tissues transmitted to plants. Interference by inhibitors, to be expected when an animal source of virus is being used, may well account for lack of transmission in this case.

The viruses causing corn-streak disease (Storey 1933), aster yellows (Black 1940, 1955), corn stunt (Maramorosch 1951), and wound tumor (Brakke, Maramorosch & Black 1953) also have been transmitted to their respective vectors from both plant and insect sources. In these earlier tests as well as in the present experiments with club-leaf virus, the needle-inoculation procedure provided a helpful technique for the study of leafhopper-borne viruses.

SUMMARY

1. Clover club-leaf virus from viruliferous *Agalliopsis novella* and from diseased *Trifolium incarnatum* plants was injected, after dilution, into 100 virus-free insects of the vector species.

2. Mechanical transmission from insect to insect and from plant to insect was successful. After an incubation period of more than 4 weeks, 6 of 22

insects inoculated with virus from insects and 3 of 17 inoculated with virus from plants became infective.

3. One hundred uninjected insects of the vector species, tested as controls, proved virus-free.

4. The mechanical transmission of club-leaf virus provides a technique for the detection and study of this virus *in vitro*.

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NUTRITION AND METABOLISM OF THE TOBACCO WILT FUSARIUM

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The wilt disease of tobacco induced by *Fusarium* was first studied by Johnson (1921), who described the causal organism as *Fusarium oxysporum* (Schlecht.) Wr. var. *nicotianae* Johnson. Subsequent studies of the disease have been centered primarily upon the development of varieties of tobacco resistant to the pathogen. Relatively little information is available concerning the physiology of the causal organism. Wolf and Wolf (1948) cultivated the fungus in a modified Richards' solution in efforts to determine the nature of the metabolic products responsible for the production of wilting. The toxic materials were not identified. It was shown, however, that at least two toxic components are involved, and that neither is identical with lycomarasmin, a toxic metabolite of the tomato wilt *Fusarium, F. lycopersici* (Clauson-Kaas, Plattner & Gäumann 1944; Plattner & Clauson-Kaas 1944, 1945).

It is the purpose of this paper to present information concerned with the nutrition of *F. oxysporum* var. *nicotianae* and its growth in a variety of synthetic media. Further, studies of some of the metabolic products of this organism have been made. These include ethyl alcohol and a red water-soluble pigment which appears in culture filtrates under certain conditions. A search has also been made for fusarinic acid, a metabolic product of other species of *Fusarium*, which has been implicated in the wilting of affected plants.

The literature concerned with the nutrition of Fusaria and with alcoholic fermentation by these organisms is so extensive that no attempt at summarization will be made. The fermentation of hexoses by Fusaria is believed by most workers to follow the same course as that by yeasts. Anderson, Everitt and Adams (1933), in studies with *F. oxysporum* from potatoes, showed that the main products of glucose metabolism are carbon dioxide and alcohol. Fermentations by Fusaria are, however, slower than with yeast, and the resulting yields of alcohol are lower, as Fusaria have a lower alcohol tolerance than does *Saccharomyces*. In a few instances, alcohol yields by Fusaria have been increased by the addition of thiamine. The explanation offered is that *Fusarium* species may be deficient in cocarboxylase (thiamine pyrophosphate), a coenzyme of the enzyme carboxylase which converts pyruvate to acetaldehyde. If cocarboxylase is deficient, fermentation can then proceed only as far as pyruvate, which accumulates in the culture filtrates. Such accumulation of pyruvate has been demonstrated (Sciarini & Nord 1944).

In the original description of *F. oxysporum* var. *nicotianae*, Johnson (1921) mentions the production of a pink pigment. Nord, Hofstetter and Dammann (1937) discovered that the pigment of *F. oxysporum* has the properties of an indicator, changing from red in acid or neutral solution to blue or purple in alkaline solution. Ashley, Hobbs and Raistrick (1937) isolated from *F. culmorum* and *F. graminearum* a pigment which they characterized chemically, and to which they gave the name rubrofusarin. Mull and Nord (1944) determined the nature of the absorption spectrum of rubrofusarin from *F. graminearum* in the ultra violet and visible regions. By comparison with the spectra of related synthetic compounds, they concluded that rubrofusarin is either 2,8-dihydroxy-1-methoxy-7-methyl xanthone or 2,3-dihydroxy-8-methoxy-7-methyl xanthone.

Fusarinic acid was originally isolated as a metabolic product of *F. heterosporum* by Yabuta, Kambe and Hayashi (1934). Its structure has been determined as 5-*n*-butyl-picolinic acid. This compound has since been found as a metabolic product of *Gibberella Fujikuroi*, *F. vasinfectum* and *F. lycopersici* (Gäumann, Naef-Roth & Kobel, 1952a, 1952b). In tomato wilt disease, these workers have shown that wilting may result from several metabolic products of *F. lycopersici*, including both lycomarasmin and fusarinic acid. Since it has been shown (Wolf & Wolf 1948) that lycomarasmin is not involved in the wilting of tobacco plants infected with *F. oxysporum* var. *nicotianae*, it became of interest to ascertain whether the toxic material produced by this fungus might be fusarinic acid.

Materials and methods. The organism studied was a strain of *Fusarium oxysporum* var. *nicotianae* isolated by Dr. F. A. Wolf from a diseased tobacco plant in Kentucky, in August, 1953. Since our previous studies (Wolf & Wolf 1948) had shown that the tobacco wilt *Fusarium* grows readily on Richards' solution, this medium was chosen as the basis of the nutritional studies. The medium contains KNO_3, 10 gm.; KH_2PO_4, 5 gm.; $MgSO_4 \cdot 7H_2O$, 2.5 gm.; $FeCl_3$, trace; glucose, 34 gm.; and distilled water, to make 1000 ml.

In the experiments with various carbon sources, the medium was modified by the omission of glucose, and to this basal medium were added various carbon sources in amounts calculated to provide 400 mg. carbon per 100 ml. (equivalent to one per cent glucose). In the experiments with nitrogen sources, Richards' solution was modified by the omission of KNO_3, and the various inorganic nitrogen sources, *L*-amino acids or nucleic acid derivatives were added to provide 25 mg. nitrogen per 100 ml. In the case of the *DL*-amino acids, this quantity was doubled, on the assumption that the *D*-isomer is probably unavailable to the fungus.

Ordinarily no pH adjustment was required in the experiments dealing with carbon sources. In the experiments in which the nitrogen source was varied, the pH was adjusted to 5.0. The media were dispensed in 33.3 ml.

quantities in 125 ml. Erlenmeyer flasks. All media were sterilized by autoclaving, and were inoculated from a spore suspension by means of sterile pipettes. Cultures were allowed to grow under stationary conditions for 9 days at room temperature. The mycelia were then removed by filtration, dried to constant weight in a desiccator over "Drierite," and weighed. pH measurements of culture filtrates were taken with a Beckman model G pH meter. Determinations of reducing sugars in the culture filtrates were performed by the Shaffer-Hartmann method. The amount of sugar consumed was determined by difference. The economic coefficient, (mat weight/sugar consumed) $\times 100$, could then be calculated (Foster 1949).

In the experiments concerned with the production of alcohol, Richards' solution was modified by increasing the glucose concentration to 10 per cent, and by adding thiamine hydrochloride at a concentration of 1.0 μgm./ml. The medium was dispensed in 100 ml. quantities in 500 ml. Erlenmeyer flasks. After inoculation, the cultures were incubated under stationary conditions for four weeks. Alcohol was determined in the neutral distillate of the culture filtrates by oxidation to acetic acid by means of potassium dichromate and phosphoric acid, distillation of the acetic acid, and titration with NaOH.

In the experiments concerned with the red water-soluble pigment produced by *F. oxysporum* var. *nicotianae*, absorption spectra of the culture filtrates were taken with a Beckman Model DU spectrophotometer. For the studies of fusarinic acid, the fungus was grown for 3 months in 500 ml. Erlenmeyer flasks containing 100 ml. quantities of Richards' solution. The attempted isolation of fusarinic acid was performed according to the procedure of Yabuta, Kambe and Hayashi (1934). Since the material isolated proved to have a melting point which differed considerably from that reported for fusarinic acid, in order to determine whether small quantities of this compound might be present, a solution of the isolated material was examined in the spectrophotometer in comparison with nicotinic acid, to determine the extent of absorption due to the pyridine ring in the region of 260–265 mμ (Stephenson 1952).

Results. Nutrition. The data concerned with the growth of *F. oxysporum* var. *nicotianae* in media containing thirty different carbon compounds as the sole source of carbon are presented in Table 1. The figures for mat weight represent the averages from two replications of the experiment; the pH readings were made upon the pooled filtrates of duplicate cultures.

It is apparent that this organism is able to utilize a great diversity of carbon compounds. Maltose and xylose supported a greater amount of growth than any other compounds tested. The polysaccharide dextrin, the trisaccharides raffinose and melezitose, the disaccharides sucrose, trehalose and cellobiose, and the monosaccharide mannose are all excellent carbon

TABLE 1. *Growth of F. oxysporum var. nicotianae in media containing various compounds as sole sources of carbon.*

Carbon Source	Mat Weight, Mg.	pH	Carbon Source	Mat Weight, Mg.	pH
Glycerol	46	5.7	Sucrose	107	5.5
Glyceraldehyde	8	4.2	Maltose	131	6.7
Phosphoglyceric Acid[1]	0	5.0	Lactose	18	4.6
Na Glycerophosphate	15	7.0	Cellobiose	103	5.6
D-Arabinose	13	4.4	Trehalose	105	6.2
L-Arabinose	65	5.8	Melibiose	22	5.7
Xylose	128	6.0	Raffinose	114	5.9
Ribose	70	6.4	Melezitose	102	6.1
Rhamnose	37	5.7	Dextrin	100	6.5
Glucose	95	6.1	Sol. Starch	56	6.2
Levulose	99	5.9	Erythritol	7	4.8
Galactose	74	5.4	Dulcitol	26	5.8
Mannose	104	6.0	Sorbitol	23	5.6
Sorbose	56	5.7	Mannitol	39	6.2
Fructose 1,6 Diphosphate[1]	17	6.4	Inositol	59	6.0

[1] Data from single cultures.

sources. Good growth was obtained in levulose, glucose, galactose and ribose, while growth was fair on *L*-arabinose, inositol, starch, sorbose, glycerol, mannitol and rhamnose. Among the sugars, *D*-arabinose, lactose and melibiose were found to be poor carbon sources for this organism.

In Table 2 are presented additional data from the same experiment, dealing with the utilization of thirteen reducing sugars. Determination of the content of reducing sugar remaining in the culture filtrates after growth of *F. oxysporum* var. *nicotianae* permitted a calculation to be made of the economic coefficient, a measure of the efficiency of conversion of substrate into cell material. After nine days, glucose, mannose and maltose had com-

TABLE 2. *The economic coefficient of F. oxysporum var. nicotianae in media containing various reducing sugars as the sole source of carbon.*

Carbon Source	Mat Weight, Mg.	Unused Reducing Sugar, Mg./100 Ml.	Sugar Consumed Mg./100 Ml.	Economic Coefficient, Per Cent
D-Arabinose	13	680	320	4.1
L-Arabinose	65	404	596	10.9
Xylose	128	104	896	14.3
Rhamnose	37	176	824	4.5
Glucose	95	0	1000	9.5
Levulose	99	424	576	17.4
Galactose	74	98	902	8.2
Mannose	104	0	1000	10.4
Sorbose	56	472	528	10.6
Maltose	131	0	1000	13.1
Lactose	18	420	580	3.1
Cellobiose	103	92	868	11.9
Melibiose	22	3	997	2.2

pletely disappeared, and only a small quantity of melibiose remained. On the basis of the quantity of sugar actually utilized, levulose is the best of the carbon sources tested, resulting in the formation of a quantity of mycelium equivalent to 17.4 per cent of the sugar consumed. This is only slightly higher than the values found for xylose and maltose, which were the best carbon sources for this fungus, considered solely from the standpoint of the quantity of mycelium produced. *D*-arabinose, lactose and melibiose, on which the organism makes poor growth, are characterized by low economic coefficients.

A series of cultures identical with those just described was prepared and incubated on a rotary shaker at a speed of 80 r.p.m. for nine days. The results will not be reported in detail, for the reason that, at least in the media used, *F. oxysporum* var. *nicotianae* appears better adapted to the semi-anaerobic conditions of stationary culture than to the aerobic conditions of shake culture. It may be stated, however, that, in general, greater growth occurs in stationary than in shake culture, while sugar utilization is more complete in shake culture. Further, these two factors are interrelated in such a way that, for any given sugar, the economic coefficient is usually higher in stationary cultures. A totally unexpected finding in the shake cultures was that *F. oxysporum* var. *nicotianae* grows principally in a yeast-like fashion, forming a white turbidity throughout the agitated solution, which, on cessation of agitation, produces a white deposit on the bottom of the flasks. On microscopic examination, the growth of the fungus was found to consist principally of single ovoid cells.

The influence of ammonium, nitrite, nitrate, and 24 different amino acids as nitrogen sources for the growth of the tobacco wilt *Fusarium* is shown in Table 3. No growth occurred in sodium nitrite in the concentration used in this experiment. The fungus utilizes both nitrate and ammonium, but these inorganic nitrogen sources are far inferior to certain amino acids. Aspartic acid, glutamic acid and β-alanine were the best of the nitrogen sources tested. Growth was likewise very good with glycine, hydroxyproline, tyrosine, serine, or tryptophane. All of the remaining amino acids were utilized, but some of them, particularly the sulphur-containing amino acids, were inferior to inorganic compounds as nitrogen sources for this organism.

Using the same basal medium as in the preceding experiment, the effect of 34 nucleic acid derivatives and related compounds as sole sources of nitrogen for the growth of *F. oxysporum* var. *nicotianae* was then studied, with the results presented in Table 4. First of all, it will be noted that none of these compounds is comparable to the best of the amino acids, namely aspartic acid, glutamic acid or β-alanine, as a nitrogen source for this organism. Ribonucleic acid, uric acid and 2,6-diaminopurine were the best of the 34 compounds tested; even with these, the amount of growth is only

one half to one third of that obtained with certain forms of amino nitrogen. As a class the pyrimidines (alloxan, barbituric acid, cytosine, 5-methyl cytosine, orotic acid, the pyrimidine moiety of thiamine, thiouracil, thymine, and uracil) are poor nitrogen sources. The purines (adenine, guanine, hypoxanthine, xanthine, uric acid, 2,6-diaminopurine) and their degradation products, allantoin and urea, are, however, good nitrogen sources. The methylated purines theobromine, theophylline and caffeine, support but little growth.

TABLE 3. *The growth of F. oxysporum var. nicotianae in media containing various inorganic nitrogen compounds or amino acids as the sole source of nitrogen.*

Nitrogen Source	Mat Weight, Mg.	pH
Ammonium sulphate	76	2.6
Sodium nitrite	0	5.3
Sodium nitrate	85	5.1
Glycine	189	3.6
β-Alanine	299	3.5
L-Aspartic acid	347	6.3
L-Glutamic acid	306	6.0
L-Asparagine	163	3.5
L-Cystine[1]	63	3.4
L-Cysteine · HCl	52	3.2
L-Leucine	79	3.8
L-Lysine · HCl	80	3.0
L-Histidine · HCl	44	3.5
L-Arginine · HCl	150	3.0
L-Tryptophane	174	3.5
L-Tyrosine[1]	181	3.4
L-Proline	115	3.5
L-Hydroxyproline	184	3.7
DL-Alanine	126	3.6
DL-Serine	175	3.7
DL-Threonine	93	3.9
DL-Valine	94	3.6
DL-Isoleucine	124	3.6
DL-Norleucine	69	3.7
DL-Phenylalanine	83	3.6
DL-Ornithine · HCl	87	3.0
DL-Methionine	75	3.3

[1] Insoluble

No significant difference is to be noted among the purines, the purine nucleosides (adenosine, guanosine, inosine, xanthosine) and the purine nucleotides (adenylic acid, guanylic acid), which are about equally effective. A different situation prevails, however, upon comparison of the pyrimidines (cytosine, uracil) with their corresponding nucleosides (cytidine, uridine) and nucleotides (cytidylic acid, uridylic acid). The nucleosides are more favorable nitrogen sources than either the nucleotides or the free pyrimidines, and compare favorably with the purines as nitrogen sources for *F. oxysporum* var. *nicotianae*.

Alcohol. The quantities of alcohol found in the cultures of *F. oxysporum* var. *nicotianae* after four weeks of growth under stationary conditions in media containing 10 gm. glucose per 100 ml. averaged 1.9 gm./100 ml. Since the theoretical yield of alcohol from 10 gm. of glucose is 5.1 gm., the conversion was 37.2 per cent of theory, on the basis of the quantity of glucose initially present. Estimations of unfermented glucose, by the Shaffer-Hartmann method, indicated a residual glucose level of 4.94 gm./100 ml. Therefore, only 5.06 gm. of glucose were utilized. Theoretically, 2.88 g. of alcohol would be expected from the fermentation of 5.06 gm. of glucose. The alcohol

TABLE 4. *Growth of F. oxysporum var. nicotianae in media containing various nucleic acid derivatives as sole sources of nitrogen.*

Nitrogen Source	Mat Weight Mg.	pH	Nitrogen Source	Mat Weight Mg.	pH
Alloxan	44	3.4	Allantoin	74	4.7
Barbituric Acid	22	4.4	Urea	82	4.8
Cytosine	48	5.7	Guanidine · HCl	56	3.6
5-Methyl Cytosine	26	4.9	2,6-Diamino-purine	103	4.2
Orotic Acid	25	3.5	8-Azaguanine	19	4.1
2-Methyl, 5-Ethoxymethyl, 6-Amino Pyrimidine	18	4.6	Adenosine	71	4.3
Thiouracil	28	3.8	Cytidine Sulphate	90	4.1
Thymine	22	4.0	Guanosine	65	3.9
Uracil	29	4.2	Inosine	61	4.0
Adenine Sulphate	87	3.7	Uridine	89	4.2
Guanine HCl	74	4.4	Xanthosine	65	4.0
Hypoxathine	69	4.0	Adenylic Acid	52	3.8
Xanthine	64	3.9	Cytidylic Acid	61	3.7
Uric Acid	106	4.1	Guanylic Acid	64	3.6
Theobromine	26	3.9	Uridylic Acid	66	4.4
Theophylline	19	4.2	Desoxyribo-nucleic Acid	79	3.8
Caffeine	25	3.9	Ribonucleic Acid	185	3.9

yield was, therefore, 66 per cent of theoretical on the basis of the glucose consumed. This would indicate that ethyl alcohol is a major metabolic product of *F. oxysporum* var. *nicotianae*.

Rubrofusarin. In the portion of the work dealing with nitrogen sources, it was noted that the culture filtrates in certain cultures of the tobacco wilt *Fusarium*, as well as the mycelial mats, were bright red in color. This occurred only in certain of the stationary cultures, especially when aspartic acid or glutamic acid was the nitrogen source, under conditions in which growth was particularly abundant. The absorption spectrum of the culture filtrate (pH 6.0) showed a well defined maximum in the visible at 500 mμ. Portions of such culture filtrates were adjusted with HCl or NaOH to pH values ranging from 1.0 to 12.0. The resulting solutions remained red from

pH 1.0 to 7.3, but changed to purple throughout the range 7.8–12.0. The pigment therefore has the properties of an indicator, the color change occurring in the region of pH 7.6. The position of maximal absorption, which was 500 mμ in acid solution, is shifted in the alkaline range to 550 mμ.

The absorption spectrum of a diluted sample of the culture filtrate of *F. oxysporum* var. *nicotianae* was also determined in the ultra violet, a maximum being located at 265 mμ. Comparison of the absorption spectrum of the pigment from *F. oxysporum* var. *nicotianae* with that of rubrofusarin (Mull & Nord 1944) indicates that the pigment of the tobacco *Fusarium* is actually rubrofusarin.

Fusarinic acid. An attempt was made to isolate fusarinic acid (5-*n*-butyl picolinic acid) from the culture filtrate of *F. oxysporum* var. *nicotianae* by the procedure given by Yabuta, Kambe and Hayashi (1934). Fifteen flasks, each containing 100 ml. of Richards' solution, were inoculated with the organism and incubated at room temperature for three months. Owing to evaporation during incubation, the pooled culture filtrates totaled only 835 ml. Small volumes of the culture filtrate were extracted with an equal volume of petroleum ether in a separatory funnel. The petroleum ether was removed, and the culture filtrate was again extracted with a second quantity of petroleum ether of equal volume. The petroleum ether solutions were pooled, and the solvent was removed by evaporation just to dryness over an electrical heater. The residue consisted of an amorphous colorless material and an orange colored oil. This residue was washed several times with ether, which removed almost all of the colored material and a considerable quantity of the colorless solid. The resulting residue of ether-insoluble substances consisted of a few milligrams of colorless apparently amorphous material, which would not crystallize from a small volume of petroleum ether. It melted at approximately 70° C., well below the reported melting point of fusarinic acid, which is 108–109° C. (Yabuta, Kambe & Hayashi 1934).

Because of the possibility that a small quantity of fusarinic acid might be present in the material isolated, an alcoholic solution of this material was examined spectrophotometrically for the absorption due to the pyridine nucleus at 260–265 mμ. A sample of nicotinic acid was examined for purposes of comparison. The results demonstrated that fusarinic acid was absent. This would apparently indicate that fusarinic acid was not produced by *F. oxysporum* var. *nicotianae* under the conditions of this experiment.

Discussion. The nutritional versatility of the tobacco wilt *Fusarium*, as shown by its ability to grow in a wide variety of synthetic media, is in general agreement with the findings reported for other species of the genus. The great majority of the sugars tested proved to be good carbon sources. Even certain pentoses such as xylose, which is not a particularly favorable

carbon source for many fungi, supported excellent growth of *F. oxysporum* var. *nicotianae*. Of the sugars tested, only *D*-arabinose, lactose and melibiose proved to be inadequate for reasonable growth. Three-carbon compounds such as glycerol, glyceraldehyde, phosphoglyceric acid and glycerophosphate were poor carbon sources, as were the sugar alcohols other than inositol. Xylose and maltose gave rise to a greater amount of growth than any other sugars, but when comparisons were made upon the basis of the amount of sugar consumed, fructose surpassed both of these sugars in the efficiency with which it is converted into cellular material. *D*-arabinose, lactose and melibiose, in which growth was poor, are characterized by very low economic coefficients.

Although the tobacco wilt *Fusarium* can utilize nitrate or ammonium nitrogen, growth is far greater when the nitrogen is provided in the form of certain amino acids. Aspartic acid was the best nitrogen source studied, but glutamic acid and β-alanine were only slightly inferior. The superiority of aspartic acid as a nitrogen source for *F. oxysporum* was noted by Anderson and Emmart (1934). Sulphur containing amino acids are notably inferior nitrogen sources for the tobacco wilt *Fusarium*.

Ribonucleic acid, uric acid, and 2,6-diaminopurine proved to be the best of 34 nucleic acid derivatives and related compounds tested as nitrogen sources for *F. oxysporum* var. *nicotianae*, though none of these was comparable to the best of the amino acids. All of the pyrimidines tested were poor nitrogen sources. In contrast, the purines were good nitrogen sources, with uric acid and 2,6-diaminopurine being especially favorable for growth. The purine degradation products, allantoin and urea, like the purines, were good nitrogen sources, but the methylated purines were very poor.

The purine nucleosides and nucleotides were comparable to the free bases in their effects upon the growth of *F. oxysporum* var. *nicotianae*. With regard to the pyrimidine derivatives, however, the nucleosides, cytidine and uridine, are considerably better than the corresponding nucleotides, cytidylic acid and uridylic acid, which are in turn better than cytosine and uracil. The findings with pyrimidines, purines, purine degradation products and methylated purines are in general agreement with data obtained on *Neurospora sitophila* (Wolf 1953). However, 2,6-diaminopurine, which is an excellent nitrogen source for *Fusarium*, completely inhibits growth of *Neurospora*. In *Fusarium*, there are no great differences between the free purines, on the one hand, and their nucleosides and nucleotides on the other, as are found in *Neurospora*. A different pattern of utilization of the pyrimidines and their nucleosides and nucleotides is also discernible in the two organisms. Little difference between the utilization of uracil, uridine, and uridylic acid was noted in *Neurospora*, while marked differences are apparent in *Fusarium*. The utilization of cytidine and uridine by *Fusarium*

surpasses that of cytidylic and uridylic acids to a significant degree, while in *Neurospora* this is not the case. Ribonucleic and desoxyribonucleic acids are utilized equally well by *Neurospora*, while ribonucleic acid is a much better nitrogen source for the tobacco wilt *Fusarium*. It seems probable that future investigations may disclose as many differences in the utilization of nucleic acid derivatives by various fungi as are already known concerning their utilization of amino acids.

With respect to the observation that growth of *F. oxysporum* var. *nicotianae* in shake cultures is yeast-like, a similar finding has been reported by Burkholder and Sinnott (1945) in an unnamed species of *Fusarium*. It would be of interest to determine what physiological alterations accompany the morphological changes induced by shake cultures. The tobacco wilt *Fusarium* appears to be unlike many fungi in growing better in stationary than in shake cultures.

The production of alcohol in considerable quantities in stationary cultures indicates that the metabolism of the organism is like that of other Fusaria in being primarily fermentative. It would seem likely that alcohol might be present to a significant extent under the semi-anaerobic conditions prevailing in the internal tissues of diseased plants.

The identification of rubrofusarin as the pigment produced by the tobacco wilt *Fusarium* adds another name to the list of species known to form this substance, which includes *F. oxysporum*, *F. culmorum* and *F. graminearum*.

The nature of the metabolite responsible for the production of wilting in diseased plants remains unknown. The evidence presented here would seem to indicate that fusarinic acid, known to be produced by *F. heterosporum*, *Gibberella Fujikuroi*, *F. vasinfectum* and *F. lycopersici*, is not formed by *F. oxysporum* var. *nicotianae*, so that this compound may be excluded from future consideration.

SUMMARY

1. The tobacco wilt fungus, *Fusarium oxysporum* var. *nicotianae*, is able to utilize a wide variety of carbon sources. Xylose, ribose, mannose, glucose, levulose, galactose, maltose, sucrose, trehalose, cellobiose, raffinose, melezitose and dextrin are satisfactory carbon sources for growth. Levulose, xylose and maltose result in the formation of more mycelium per gram of sugar utilized than certain other sugars. *D*-arabinose, lactose and melibiose are poorly utilized.

2. *F. oxysporum* var. *nicotianae* can utilize nitrate, ammonium or amino nitrogen. Growth on certain amino acids, notably aspartic acid, glutamic acid or β-alanine, is far superior to that obtained on inorganic nitrogen sources. Growth of the fungus was studied using 34 nucleic acid derivatives

as nitrogen sources. Ribonucleic acid, uric acid and 2,6-diaminopurine were the most effective, although none were comparable to the best of the amino acids. Purines, purine nucleosides and nucleotides, pyrimidine nucleotides, allantoin or urea were better nitrogen sources for this organism than methylated purines, pyrimidines, or pyrimidine nucleotides.

3. In shake cultures, *F. oxysporum* var. *nicotianae* grows in a yeast-like fashion.

4. Ethyl alcohol is a major metabolic product of glucose fermentation.

5. In culture filtrates a red water-soluble pigment is produced which has the properties of an indicator. This pigment has been identified as rubrofusarin.

6. Attempts to isolate fusarinic acid (5-*n*-butyl picolinic acid) from culture filtrates were unsuccessful.

The writer desires to express his appreciation to Dr. Arthur P. Harrison, Dept. of Biology, Vanderbilt University, for assistance with the alcohol determinations, and to Mr. Paul Scott, Dept. of Chemistry, Vanderbilt University and Dr. Marcus Hobbs, Dept. of Chemistry, Duke University, for carrying out the ultra violet spectrophotometric examinations of rubrofusarin and fusarinic acid, respectively.

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THE STATUS OF THE GENUS ANDERSSONIOPIPER TRELEASE

T. G. YUNCKER

In 1934, Trelease published a new monospecific genus of the Piperaceae founded on a collection made by N. J. Andersson in "Panama" in 1852. This plant showed characteristics strongly in contrast with other American species of the family. The character noted by Trelease which prompted him to believe that he had a new genus was the production of "flabellately umbellate axillary spikes." The additional fact that the plant was dioecious was not mentioned in his description and presumably was not recognized by him. Had this character, coupled with the position and number of the spikes, been known, it is probable that Trelease would have come to some other conclusion relative to the relationship of Andersson's plant. Dioecism is distinctly a character of Old World species while American species have perfect flowers.

Trelease had some doubts regarding the accuracy of the data on the label with respect to the origin of the specimen, if not the validity of his new genus. He states: "While this new genus is clearly distinguishable from all other known genera of Piperaceae, its rediscovery must be awaited with more than usual interest, because there are reported contradictions in the labeling of Andersson's collections, so that while its characters are firmly established, the exact geographic source of the genus now named for him requires confirmation."

In a review of the Panamanian species of the Piperaceae which I presented in 1950, I somewhat reluctantly followed Trelease in his treatment of this entity. At that time I had not had the opportunity of examining the type specimen of Trelease's genus. Recently, through the courtesy of the Botanical Museum, I have received on loan from Stockholm 8 sheets, all bearing what are obviously the same species and all with Andersson's labels. One of these sheets is the one seen originally by Trelease. This sheet has on its label "Panama, Apr. 1852, N. J. Andersson" and "Pothomorphe" in a different handwriting. In addition, Trelease has added "Anderssoniopiper panamense n. gen. & sp. W.T." It was the custom of Trelease to annotate or initial all sheets which he examined but there is no evidence on any of the other 7 sheets that they ever were seen by him. There is a second sheet with the same data which has been annotated "Anderssoniopiper panamense Trel." by someone but not in Trelease's handwriting. The specimen seen by Trelease bears pistillate spikes while those on this second "Panama"

specimen are staminate. Four of the sheets have labels with "Tahiti, Sept. 1852," one has "Honolulu" without date, and the other has "Sidney, N. Hollandia, Oct. 1852."

These eight sheets are, without much doubt, to be considered as representing *Piper latifolium* L. f. The four sheets carrying Tahiti as the locality are presumably properly labelled. It is highly doubtful if this species occurs in Panama as no subsequent collector, so far as known, has found anything like it there. It is not known from Hawaii where there are no indigenous species of Piper. It is also questionable if it was obtained in "N. Hollandia" [Australia].

To the writer, there appears to be little doubt but that labels bearing the names of the various places visited by Andersson were indiscriminately attached to specimens presumably all obtained in Tahiti in September of 1852. If this conclusion is correct, the genus Anderssoniopiper becomes an addition to the already rather lengthy list of synonyms of the genus Piper.

For discussions of the nomenclatural status of the binomials *P. latifolium* L. f. and *P. methystichum* Forst. f., which have been confused by some writers, see J. W. Moore, 1934, and A. C. Smith, 1943.

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STUDIES IN THE GENUS DODECATHEON OF NORTHWESTERN AMERICA

KATHERINE I. BEAMISH[1]

Dodecatheon, a member of the family Primulaceae, is a familiar part of the spring flora in some sections of British Columbia and surrounding areas. Representatives of the genus in the northwest are found along the coast islands and parts of the mainland from Oregon to Alaska. East of the Coast Range they cross southern British Columbia to Alberta and Saskatchewan. Several of the species occur also in eastern Washington, Idaho, and Montana, and some of them still farther south. Habitats vary from sea level to high altitudes and from salt water marshes or the edges of mountain streams to arid slopes where drought conditions prevail in summer.

All species of the genus are perennial and spring-blooming. They have basal leaves and simple scapes, each scape with an umbel of one to twenty-five flowers. The most striking floral characteristics are the reflexed perianth, the protruding stamens, and the scalloped marking on the corolla throat of almost every flower.

The genus *Dodecatheon* in North America has been treated biosystematically by Thompson (1953). He divides it into three sections, *Purpureo-tubulosa*, *Capitulum*, and *Dodecatheon*. Each section is subdivided into species and subspecies. Chromosome numbers, hybridization, and field studies have all been used to aid in determining relationships. Thompson points out, however, that these aids to classification have been most readily available for the section *Purpureo-tubulosa* as represented in California. Less intensive investigations were made in the section *Capitulum* and the studies in the section *Dodecatheon* were limited mainly to herbarium specimens. The present paper offers new information concerning all three sections as they occur in northwestern America. The findings reported are the result of field and herbarium studies, cytological examinations, and plant collections over a wide area.

Methods. As the area covered is large, field work has been confined to southwestern and south central British Columbia and to one location in northern Washington. Most of the northwestern species and subspecies have been studied in their native habitats, some in a number of locations. Plants of all species dealt with and from as many populations as possible have been collected personally or contributed by interested friends whose help has been invaluable. The plants were grown in the botanical garden of the University

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of British Columbia. The collections included the more eastern and northern species and subspecies which have not been observed in the field. Approximately 800 pressed specimens have been studied in detail. These were kindly made available by the curators of the following herbaria: Provincial Museum, Victoria, British Columbia (V); National Museum of Canada, Ottawa (CAN); Gray Herbarium, Harvard University, Cambridge, Massachusetts (GH); University of California, Berkeley (UC); University of Washington, Seattle (WTU); University of British Columbia, Vancouver (UBC).

Chromosome counts have been made for all of the northwestern species and the same species has been checked from as many locations as possible. Microsporogenous tissue proved to be the most satisfactory material for a

TABLE 1. *Chromosome counts for the northwestern species and subspecies of Dodecatheon, listed according to the type of cell division from which they were made.*

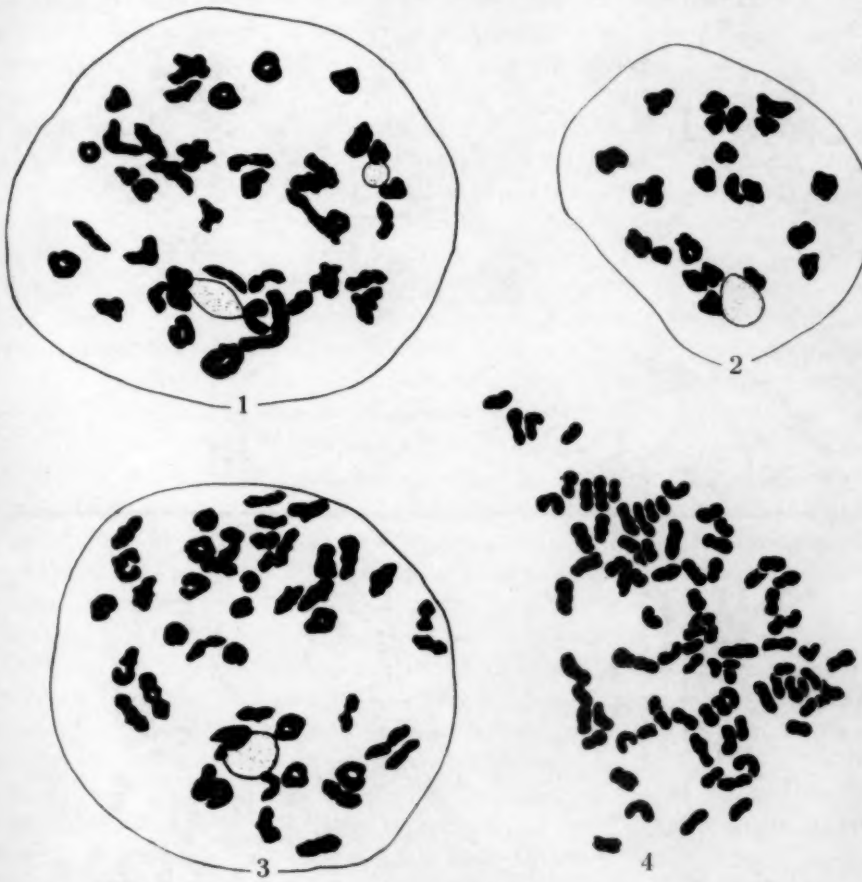
Species or Subspecies	Locality	Mitotic (2n)	Meiotic (n)	Fig.
D. hendersonii subsp. hendersonii	Duncan, B. C.		ca. 44	
	Victoria, B. C.		ca. 44	1
D. conjugens subsp. viscidum, eastern form	Natal, B. C.		22	
D. frigidum	Sable Pass, Alaska		22	2
D. jeffreyi subsp. *jeffreyi*	Stevens Pass, Wash.		22	5
	Prince Rupert, B. C.		43	6
	Vancouver Island, B. C.	ca. 86		4
	Douglas Island, Alaska		ca. 43	
D. dentatum subsp. dentatum	Penticton, B. C.	ca. 44		
D. cusickii	Penticton, B. C.		22 + 1	
	Princeton, B. C.		22 + 1	8
D. radicatum subsp. *radicatum*	Mortlach, Sask.		22	7
	Fairmont Springs, B. C.	ca. 44		
	Dutch Creek, B. C.	ca. 44		
D. radicatum subsp. *macrocarpum*	Victoria, B. C.		ca. 66	
	Lulu Island, B. C.		ca. 44	3
	Anchorage, Alaska		ca. 44	

study of the chromosomes but even under the best conditions their small size and large numbers made exact counts difficult to obtain. Where flowers were not available, root tips were substituted. Two hours' prefixation in paradichlorobenzene (Meyer 1945) contracted mitotic chromosomes sufficiently that they could be counted with reasonable assurance. For all counts aceto-carmine squashes were made from material fixed in a mixture of alcohol and acetic acid, 3:1. Ferric chloride added to the aceto-carmine intensified the stain.

Discussion of individual species. The systematic treatment of the genus *Dodecatheon* presented by Thompson covers adequately, as far as available information goes, most of the northwestern species. Evidence from the present study warrants only one immediate change though it reveals factors which may be the basis of future changes.

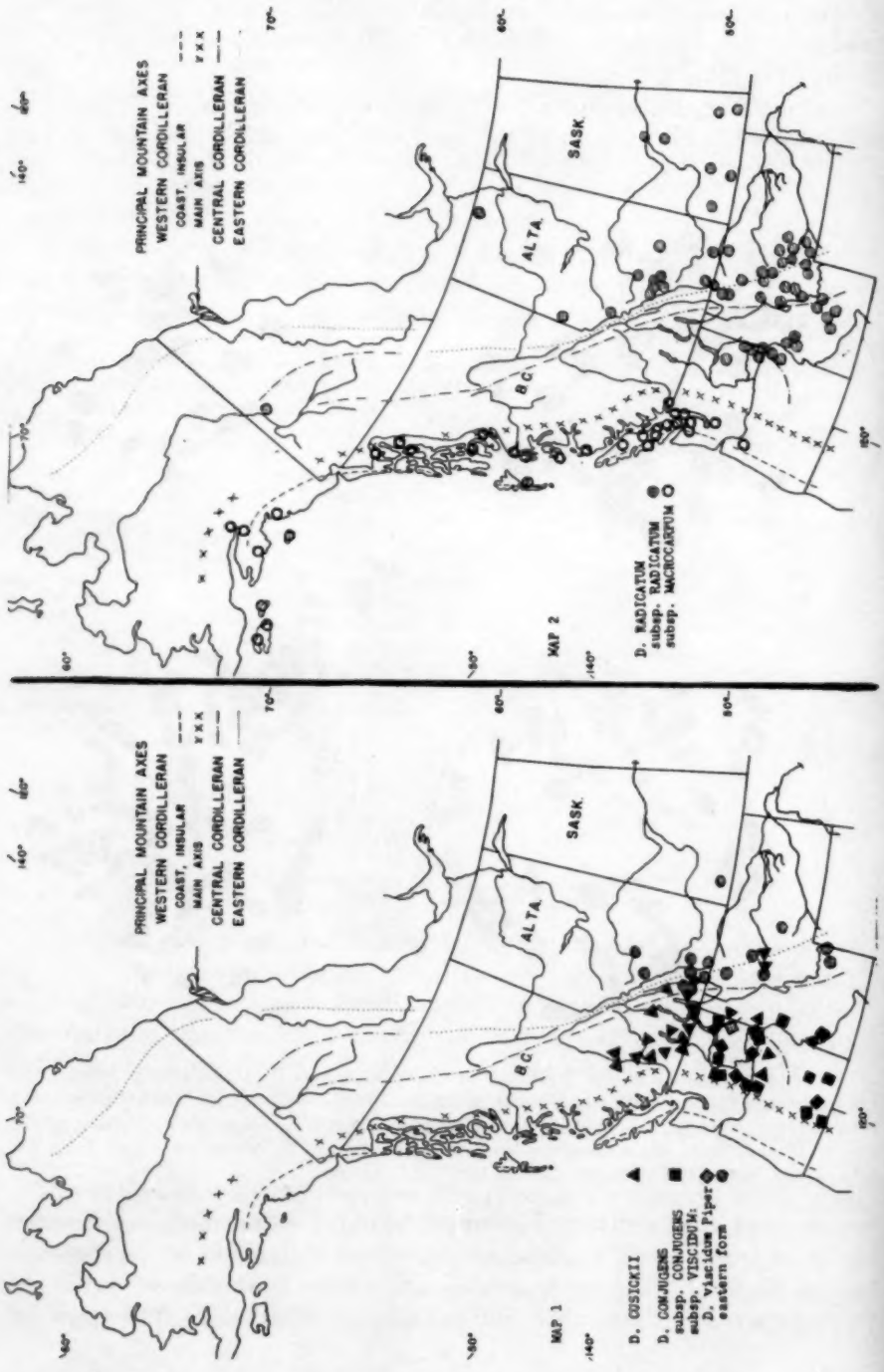
The species are discussed individually using, with one exception, the nomenclature established by Thompson (1953). Chromosome counts obtained are listed in table 1.

Section Purpureo-tubulosa. 1. *Dodecatheon hendersonii* A. Gray subsp. *hendersonii* has been found in the northwest only along the coast and no



FIGS. 1–4. Camera lucida drawings of division figures in *Dodecatheon* species and subspecies, ×1300. FIGS. 1–3. Meiosis. FIG. 4. Mitosis. FIG. 1. *D. hendersonii* subsp. *hendersonii*, Duncan, B. C., n = ca. 44. FIG. 2. *D. frigidum*, Sable Pass, Alaska, n = 22. FIG. 3. *D. radicatum* subsp. *macrocrapum*, Lulu Island, B. C., n = ca. 44. FIG. 4. *D. jeffreyi* subsp. *jeffreyi*, Vancouver Island, B. C., 2n = ca. 86.

farther north than southern Vancouver Island. Two colonies on Vancouver Island, at Duncan and Victoria, are tetraploid with about 88 chromosomes (n = ca. 44, fig. 1). Pairing at meiosis is irregular as evidenced by the frequent occurrence of univalent and multivalent associations. Thompson re-



MAPS 1–2. Ranges of *Dodecatheon* species. Specific names are indicated on the maps.

ports 44-, 66-, and about 132-chromosome populations of this subspecies in California.

2. *Dodecatheon conjugens* Greene subsp. *viscidum* (Piper) H. J. Thompson is a taxonomic entity which may need future revision. According to Thompson it comprises two forms which he leaves unnamed, one in eastern Washington with heavy glandular pubescence throughout and one in "Canada and western Montana" with glandular pubescence only on the leaves and lower scape. The evidence against Thompson's treatment of the two forms is given below.

The western form, to which the name *D. viscidum* was first applied, was described by Piper (1901) from Spangle, Washington. It bears many of the characteristics of *D. conjugens* subsp. *conjugens,* including dark purple anthers 6.0–7.0 mm. long, but the densely glandular-pubescent inflorescence is that of *D. cusickii.* Piper's *D. viscidum* is apparently uncommon since few examples of it appeared in the hundreds of specimens examined, and those few were all from a small area around the type locality (map 1). Finally, the original *D. viscidum* occurs where *D. conjugens* subsp. *conjugens* and *D. cusickii* overlap in range. It may well be only a sporadically-occurring hybrid between the two. The chromosome number is unknown.

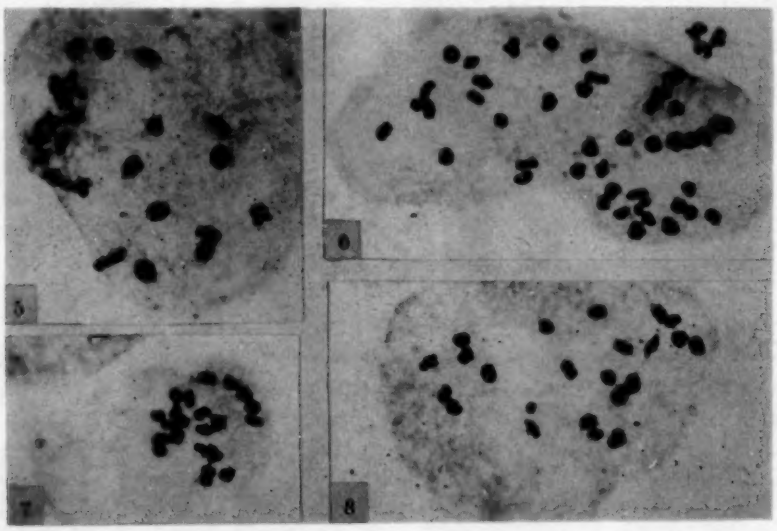
The eastern form of Thompson's *D. conjugens* subsp. *viscidum* is undoubtedly the taxon *D. pubescens* described by Rydberg (1900) from Montana and included by Thompson under subsp. *viscidum.* It has yellow-tipped anthers 4.5–5.5 mm. long and only scattered hairs in the inflorescence. It covers a wide range in Montana, southeastern British Columbia, southern Alberta, and southwestern Saskatchewan (map 1). This form is undoubtedly a subgroup of *D. conjugens* though possibly unrelated to Piper's *D. viscidum.* Representatives from Natal, British Columbia, have 44 chromosomes.

In spite of differences between the two forms in morphology and range only field and cytogenetic studies can determine with certainty the relationships within Thompson's *D. conjugens* subsp. *viscidum.*

3. *Dodecatheon frigidum* Cham. & Schlecht. occurs in Alaska, Yukon, and northern British Columbia. It has been reported also from the Asiatic coast (Gray 1876). Plants from Sable Pass, McKinley Park, Alaska, possess 44 chromosomes (n = 22, fig. 2). Thompson reports 44 as the somatic number for specimens from one location on the north slope of the Brooks Range, Alaska.

Section Capitulum. 1. *Dodecatheon jeffreyi* Van Houtte subsp. *jeffreyi* ranges in the northwest from Montana, Idaho, and Washington via the British Columbia coast to Alaska. Plants from Stevens Pass in Washington are diploid with 44 chromosomes (n = 22, fig. 5). Thompson has found this subspecies to be diploid also in California though there it has 42, 44, or occasionally 43 chromosomes. Plants from a colony on Vancouver Island, one

at Prince Rupert, British Columbia, and one on Douglas Island, Alaska, are tetraploids. Those from Prince Rupert have 86 chromosomes (n = 43, fig. 6). The pairing during meiosis is very regular. Approximately the same numbers of chromosomes were found in the material collected at the other locations (Vancouver Island, fig. 4). Morphologically the plants of the various colonies are not consistently different in spite of the difference in degree of polyploidy. Aware of diploids only in this group, Thompson treats *D. jeffreyi* subsp. *jeffreyi* as one large variable taxon. The additional evidence of polyploidy presented here is not considered sufficient basis without consistent morphological differences for subdivision of the unit.



FIGS. 5–8. Photomicrographs of meiotic divisions in *Dodecatheon* species and subspecies, ×980. FIG. 5. *D. jeffreyi* subsp. *jeffreyi*, Stevens Pass, Wash., n = 22. FIG. 6. *D. jeffreyi* subsp. *jeffreyi*, Prince Rupert, B. C., n = 43. FIG. 7. *D. radicatum* subsp. *radicatum*, Mortlach, Sask., n = 22. FIG. 8. *D. cusickii*, Princeton, B. C., n = 22 + 1.

Section Dodecatheon. 1. *Dodecatheon dentatum* Hook. subsp. *dentatum* is found east of the Western Cordillera in Washington, Idaho, and southern British Columbia. Specimens from Penticton, British Columbia, have approximately 44 chromosomes. This number is in agreement with that reported by Thompson (1953) for plants from Chelan County, Washington, and from Multnomah County, Oregon.

2. *Dodecatheon cusickii* Greene grows most commonly in British Columbia, Washington, and Idaho between the Western and Eastern Cordillera. It has been found also in Montana on the eastern side of the mountains. Thompson has found 44 chromosomes in specimens from Whitman County, Washington. Plants from Penticton and Princeton, British Columbia, have as a

rule 45 chromosomes (n = 22 + 1, fig. 8). An occasional cell undergoing meiosis has what appears to be 23 pairs plus 1 univalent. The discrepancy may be due to the precocious separation of one pair.

3. *Dodecatheon radicatum* Greene as treated here includes three subspecies, two of which are common in the northwest: 3a. *D. radicatum* subsp. *radicatum*. Anthers 3.5–5.0 mm. long, about twice as long as the filaments, plants of the Rocky Mountains and eastern regions. 3b. *D. radicatum* subsp. *macrocarpum*. Anthers 5.5–7.0 mm. long, more than twice as long as the filaments, plants of the Pacific Coast.

3a. *Dodecatheon radicatum* Greene subsp. *radicatum* is found in the northwest east of the main axis of the Western Cordillera (map 2). One herbarium specimen, Eastwood 84, May 20, 1914, from Moosehide, Yukon Territory, is classed as *D. radicatum* subsp. *radicatum* because of its floral characteristics. Its apparent isolation from other populations of the same subspecies may be due only to lack of collections in the intervening area. The population from which it comes is unknown cytologically. Plants of three colonies from which chromosome counts have been made are all diploids. Specimens from Mortlach, Saskatchewan, possess 44 chromosomes (n = 22, fig. 7). Those from Fairmont Springs and Dutch Creek, British Columbia, each proved to have approximately 44.

3b. **Dodecatheon radicatum** Greene subsp. **macrocarpum** (Gray) Beamish, comb. nov. *Dodecatheon Meadia* L. var. *macrocarpum* Gray. Geol. Surv. Cal. Bot. 1: 467, 1876. *Dodecatheon macrocarpum* (Gray) Knuth. Pflanzenreich 4: 241, 1905. *Dodecatheon superbum* Pennell and Stair. Bartonia 24: 20, 1946. *Dodecatheon macrocarpum* (Gray) Knuth var. *alaskanum* Hulten. Fl. Alaska and Yukon 8: 1289. 1948.

Thompson (1953) considers the two subspecies of *D. radicatum* (3a and 3b) as both belonging to the former taxon, *D. radicatum* subsp. *radicatum*. His decision is based on morphology alone. The present investigation has disclosed that the Pacific Coast populations are polyploid in contrast with the diploid condition of the inland representatives. Specimens from Victoria, Vancouver Island, have approximately 132 chromosomes (n = ca. 66); those from Lulu Island, near Vancouver, and from Anchorage, Alaska, have approximately 88 chromosomes (n = ca. 44, Lulu Island, fig. 3). Still, the two subspecies together would form a large and variable group comparable to *D. jeffreyi* subspecies *jeffreyi*. However, in addition to the difference in degree of polyploidy within *D. radicatum* there is also a small but consistent difference in stamen morphology between coast and inland populations. The total evidence suggests that the polyploids have become geographically separated from the diploids and have begun to differentiate from the parent species.

For *D. radicatum* subsp. *radicatum*, Thompson has given a detailed de-

scription which holds also for *D. radicatum* subsp. *macrocarpum* except for the difference in stamen morphology noted in the key above.

Neotype: Dall s.n., June 2, 1874, Middleton I., Alaska.

Type locality: from Alaska southward.

Distribution: along the coast and on the coast islands from Oregon to Alaska (map 2).

Representative specimens examined: ALASKA. Juneau, Frohne, 4965 (UBC); Eklutna Flats, Frohne 4945 (UBC); Deep Bay, Admiralty I., Eyerdam 3016 (UC); Raspberry I., Kodiak group, Eyerdam 3683 (WTU, CAN); Cordova, Eyerdam s.n., Aug. 1932 (WTU); Seward, Anderson 6745 (CAN); Middleton I., Alaska Terr., Dall s.n., June 2, 1874 (neotype, GH.). BRITISH COLUMBIA. Limestone I., Queen Charlotte I., Newcombe s.n., June 19, 1913 (UBC); Larson Harbor, Banks I., McCabe 7329 (UC); Calvert I., McCabe 4082 (UC); Sayward, Vancouver I., Krajina s.n., June 3, 1950 (UBC); Millstream, Nanaimo, Macoun s.n., July 1, 1914 (V); Alberni, Vancouver I., Henry s.n., June 26, 1916 (UBC); Lulu I., Beamish 49102 (UBC); Uplands, Victoria, Beamish 49101 (UBC); Comox, Anderson s.n., May 18, 1899 (V). WASHINGTON. American Lake, Todd s.n., May 11, 1908 (WTU); Goose Rock, Whidbey I., Smith 66 (UC); Lummi Rocks, Muenscher 9720 (UC, WTU, UBC). OREGON. Columbia R. near Multnomah Falls, Anderson s.n., May 8, 1936 (UC).

Nomenclature in the subspecies *macrocarpum* has presented a problem. The taxon was first described by Gray (1876) as *D. meadia* var. *macrocarpum*. No type was designated but after the description Gray stated:

> —A form which may be referred here, with laciniately-toothed spatulate leaves, was collected on the mountains of Ventura Co., Brewer.

On a label which reads "Syn. Fl. N. Amer." Brewer's specimen from the Gray Herbarium has been annotated, presumably by Gray, *D. Meadia* var. *macrocarpum, laciniatum*. Clearly Gray considered this specimen to be an anomaly in the taxon or at best a form of var. *macrocarpum*. Another specimen from the Gray Herbarium, Dall s.n., June 2, 1874, Middleton I., Alaska Terr., has been annotated on a similar label by the same hand simply *D. Meadia* var. *macrocarpum*.

Thompson (1953) has chosen the Brewer specimen as the type of *D. meadia* var. *macrocarpum* and because he identified this specimen as *D. clevelandii* subsp. *sanctarum* of California, the epithet *macrocarpum* was placed in the synonomy of that group. Thompson's identification of Brewer's specimen is undoubtedly correct but his choice of the specimen as the type of *D. meadia* var. *macrocarpum* apparently results from a misinterpretation of Gray's written words. Therefore, under Article 18 *bis* of the International Code of Botanical Nomenclature, the Dall specimen from Middleton Island has been chosen as the neotype and the epithet *macrocarpum* has been retained.

3c. *Dodecatheon radicatum* Greene subsp. *watsonii* (Tidestrom) H. J. Thompson is found at high elevations. One population of small alpine plants has been observed on Mt. Copley, Vancouver Island. On the basis of morphology alone this group has been identified by Thompson as *D. radicatum* subsp. *watsonii*.

Discussion. The genus *Dodecatheon* is a polyploid complex ranging over a large part of North America. Its polyploidy was established by Thompson (1953) on the basis of chromosome counts for the western species, chiefly Californian, and three counts for northwestern species. It is now confirmed by additional counts for the northwestern species. Thompson reports diploids, triploids, tetraploids, and hexaploids in California. Diploids, tetraploids, and hexaploids occur in the northwest but no triploids have as yet been found.

According to present information the distribution of polyploidy in the northwest follows a definite pattern. Diploids occur east of the Western Cordillera. These include *D. conjugens* subsp. *viscidum*, *D. jeffreyi* subsp. *jeffreyi*, *D. dentatum* subsp. *dentatum*, *D. cusickii*, and *D. radicatum* subsp. *radicatum*. Polyploids follow the coast and the coastal islands from northern Oregon to Alaska. In this group are *D. hendersonii* subsp. *hendersonii*, *D. jeffreyi* subsp. *jeffreyi*, and *D. radicatum* subsp. *macrocarpum*. The chromosome number for *D. radicatum* subsp. *watsonii* is undetermined. Only the diploid *D. frigidum*, with its distribution over both coastal and inland areas of the far northwest, is known to vary from the pattern.

Two points of interest, both of which are evident in Thompson's work, are emphasized in the present study:

1. Polyploidy alone has had little effect on morphology. *D. jeffreyi* subsp. *jeffreyi*, diploid and tetraploid, forms one large variable group lacking sufficiently distinctive populations to warrant subdivision. The diploid *D. radicatum* subsp. *radicatum* and the polyploid *D. radicatum* subsp. *macrocarpum* are as yet morphologically differentiated in only a minor way. Moreover, the tetraploid and hexaploid populations of *D. radicatum* subsp. *macrocarpum* present no consistent visible differences.

2. Small variations in chromosome numbers likewise produce no outstanding morphological effects. *D. jeffreyi* subsp. *jeffreyi* again serves as one example. The 44-chromosome diploid of Stevens Pass, Washington, and the 43-pair tetraploid of Prince Rupert, British Columbia, differ not only in degree of polyploidy but also in their basic complement. Yet they are not morphologically distinct.

D. cusickii is a second example. Plants from two locations in British Columbia have one extra univalent chromosome which is evidently missing from the 22-chromosome population occurring in Whitman County, Washington (Thompson 1953). Yet *D. cusickii* is morphologically a reasonably uniform species.

Sufficient cytological work has been done in the genus *Dodecatheon* to show that many alterations in chromosome numbers have occurred. The changes run from gain or loss of a single chromosome to duplications of whole complements. The effects of such changes are not morphologically distinctive. Perhaps they lie in the provision of isolation between populations, either mechanical isolation through spread of certain groups to new territories or genetic isolation through inability of adjacent populations to produce fertile hybrid plants. Only cytogenetic studies can now determine in greater detail the present relationships and the possible course of speciation within the genus.

SUMMARY

1. The genus *Dodecatheon* in northwestern America is a polyploid complex ranging over a large part of British Columbia and surrounding areas.

2. Field and herbarium studies, plant collections, and cytology have revealed factors pertinent to the present classification of the genus. These factors have been discussed.

3. One new combination, **D. radicatum** subsp. **macrocarpum**, has been established.

4. Chromosome numbers have been listed in table form.

5. The diploids occur east of the Western Cordillera; the polyploids along the coast and coastal islands from northern Oregon to Alaska. Only the diploid *D. frigidum* of the far north has both coast and inland distribution.

6. Changes in chromosome number, either of single chromosomes or of whole complements, are not always correlated with morphological distinction. They may serve as isolating mechanisms in the process of speciation.

Sincere gratitude is expressed for the assistance and advice of Dr. V. C. Brink and Dr. T. M. C. Taylor under whose guidance the author worked as a graduate student.

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THE CYTOLOGY OF XANTHISMA TEXANUM D. C. II. ADDITIONAL CHROMOSOME TYPES[1]

E. R. WITKUS, T. J. LOWERY & C. A. BERGER

Populations of *Xanthisma texanum* D.C., were reported (Berger & Witkus 1954) to contain two types of plants. One type had 4 bivalents (fig. 1) at the first meiotic division and eight chromosomes in the cells of the shoot, while the other type had 5 bivalents (fig. 2) at the first meiotic division and ten chromosomes in the cells of the shoot. Both types had eight chromosomes in the cells of the roots and were indistinguishable in external morphology. The extra, or supernumerary, chromosome was visibly different from the other four chromosomes of the haploid set and was designated Chromosome V.

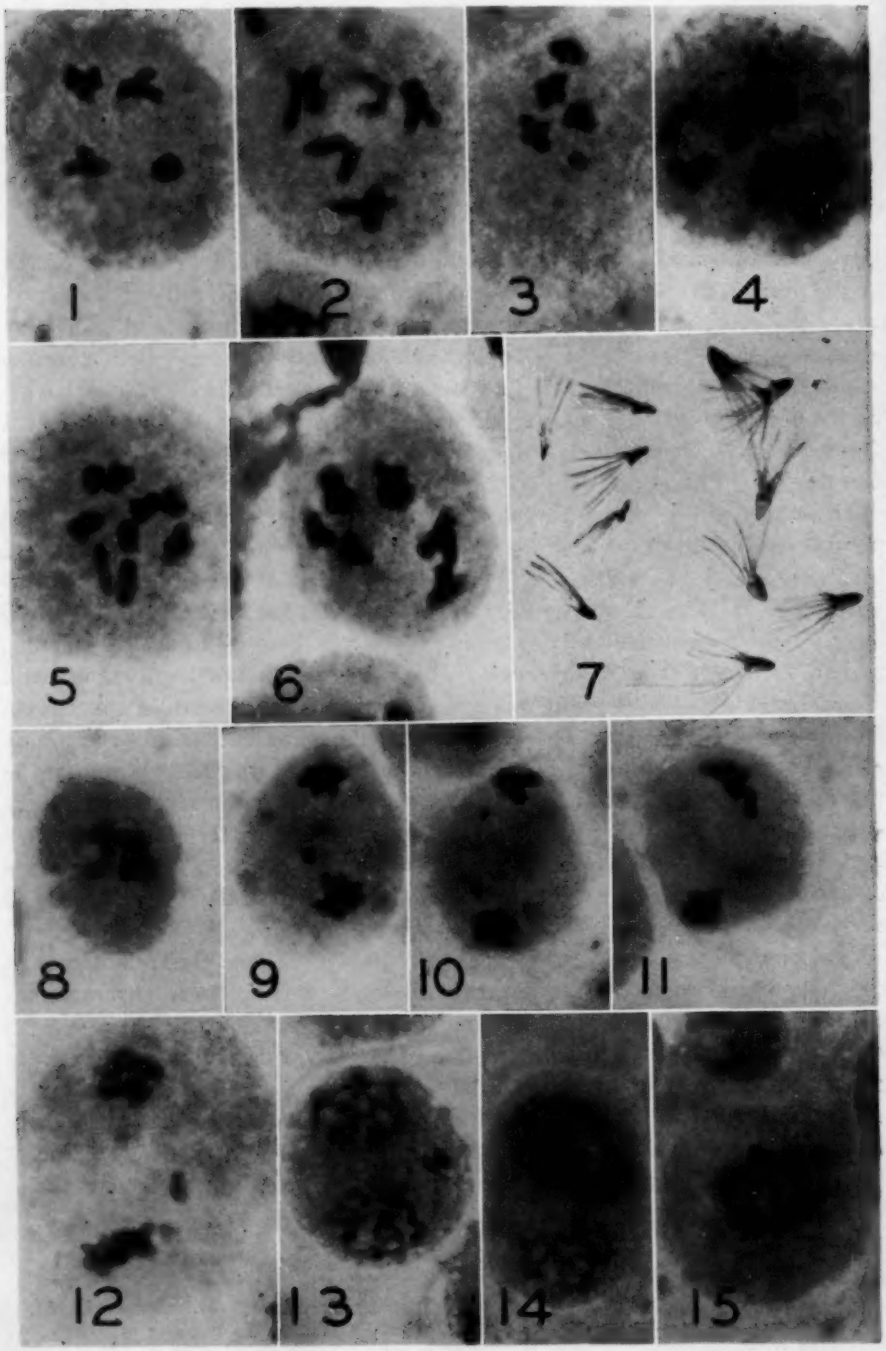
Further studies have revealed three additional types of plants, one having 4 bivalents and 1 univalent at meiosis (fig. 3), another having 5 bivalents and 1 univalent (fig. 4) and the third a tetraploid with 9 bivalents (fig. 5). The frequency of these types in a population of 100 unselected plants was as follows: 35 plants had 4 bivalents; 32 had 5 bivalents; 27 had 4 bivalents and 1 univalent; 5 had 5 bivalents and 1 univalent; and 1 had 9 bivalents.[2] This plant was evidently a tetraploid form of the 4 bivalent and 1 univalent type. The seeds produced by these different type plants were fertile with the exception of the nine bivalent plant. Apparently the presence of the supernumerary chromosome does not impair the fertility of the seeds. On the other hand the seeds obtained from the polyploid plant were all sterile. Figure 7 shows the size difference between the viable seeds of a 4 bivalent and 1 univalent plant and the much smaller sterile seeds of the polyploid.

All of these types of plants, except the tetraploid, had 8 chromosomes in the cells of the roots. In the plants with the supernumerary chromosomes occasional root cells were found with 9 or 10 chromosomes. These cells never constituted more than about 2% of the dividing cells and they were most frequent in the 5 bivalent and 1 univalent plants. They probably represent cells in which the process of chromosome elimination failed in early development.[3] Similar slight variations in chromosome number were found in the shoot with about the same frequency. These variations always involved only the supernumerary chromosomes.

[1] This investigation was aided by a Grant (G1149) from the National Science Foundation.

[2] Recently a single plant of another type has been found with 6 bivalents (fig. 6).

[3] The data on variation in chromosome number is largely the work of R. T. Cronin contained in his unpublished M.S. Dissertation (Fordham 1955).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Microsporogenesis. In the 4 bivalent and in the 5 bivalent plants, microsporogenesis was normal in all respects. In 4 bivalent and 1 univalent plants the meiotic behavior of the univalent was different in different anthers. In some anthers all the cells showed the univalent undergoing a reductional division, i.e. passing undivided to one pole (fig. 8). In other anthers the univalent lagged somewhat at anaphase I and in some cells it divided equationally (figs. 9 & 10) while in others it passed undivided to one pole (fig. 11). Rarely single anthers were found in which the univalent not only lagged (fig. 12) but was eliminated at the first division (fig. 13) and was present as a micronucleus during the second division (fig. 14). When this condition was found it was present in most of the microsporocytes of that anther. In 5 bivalent and 1 univalent plants the three supernumerary chromosomes usually formed one bivalent and one univalent (fig. 15). Usually the univalent passes undivided to one pole. Occasionally the three supernumeraries were present as a trivalent or as three univalents (fig. 16).

A study of microsporogenesis in the tetraploid plant revealed many multivalent associations at diplotene and diakinesis. Of 200 cells studied, 64% had nine bivalents (fig. 5); 15% had seven bivalents and one quadrivalent (fig. 17); 8% had five bivalents and two quadrivalents (fig. 18); 5.5% had three bivalents and three quadrivalents (fig. 19); 4% had four quadrivalents and one bivalent (fig. 20); 2% had six bivalents, one quadrivalent and two univalents (fig. 21); .5% had five bivalents, two trivalents and two univalents; .5% had six bivalents, one trivalent and three univalents; and .5% had eight bivalents and two univalents. The multivalent associations always involved the four chromosomes present in 4 bivalent plants. The supernumerary chromosome, Chromosome V, was never involved in a multivalent association. In spite of the frequent multivalent associations at diplotene and diakinesis, separation at Anaphase I was normal and nine univalent chromosomes moved to each pole. Rarely the supernumeraries lagged at Anaphase I and formed micronuclei.

Pollen grain divisions. The first pollen grain division in the tetraploid as well as in the other types occurred after the tetrads had separated and each cell had acquired a thick spore wall. The divisions were normal in all

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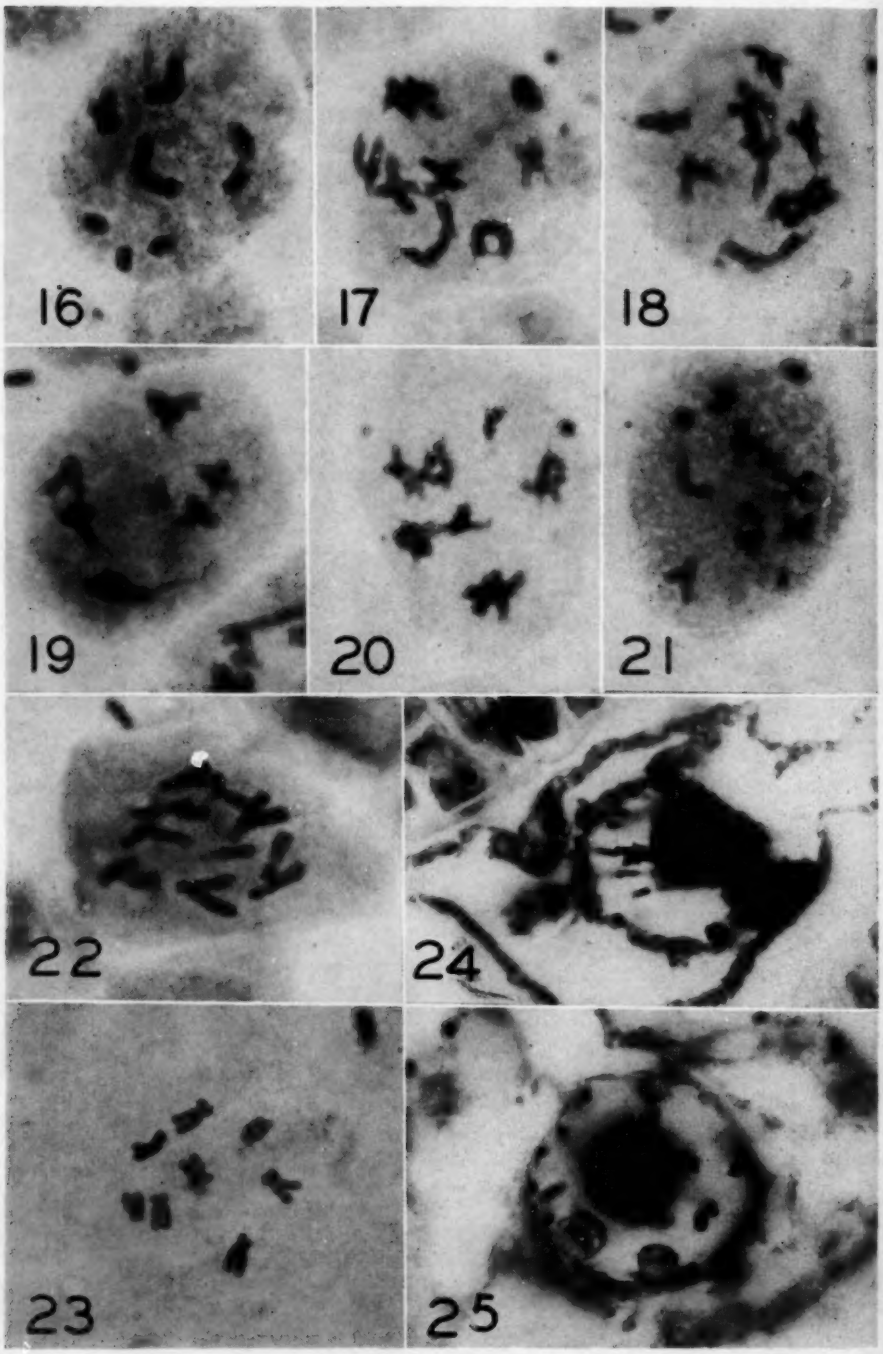
FIGS. 1–15. All figures except figure 7 are photomicrographs of aceto-orcein smear preparations of microsporocytes in various stages of division from the different plant types of *Xanthisma texanum*. Magnification × 1500. FIG. 1. 4 bivalents. FIG. 2. 5 bivalents. FIG. 3. 4 bivalents and 1 univalent. FIG. 4. 5 bivalents and 1 univalent. FIG. 5. 9 bivalents. FIG. 6. 6 bivalents. FIG. 7. Fertile seeds of 4 bivalent and 1 univalent plant and sterile seeds of the tetraploid plant with 9 bivalents. FIG. 8. Univalent undergoing reduction. FIGS. 9 & 10. Univalent dividing equationally. FIG. 11. Univalent undergoing reduction. FIG. 12. Lagging univalent. FIG. 13. Elimination of univalent. FIG. 14. Univalent micronucleus. FIG. 15. The supernumeraries as 1 bivalent and 1 univalent.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respects including the behavior of the supernumerary chromosome.

Adventitious roots. Cuttings were made of the shoots of the different plant types and the adventitious roots studied to determine their chromosome content. In the case of the diploid types of plants the adventitious roots had the same chromosomal conditions as present in the shoot. In the tetraploid plant, however, of the seventeen roots studied six had sixteen chromosomes in all their cells (fig. 22) and eleven had eight chromosomes (fig. 23). It was concluded that the tetraploid plant was a mosaic of diploid and tetraploid tissue.

Embryos of the tetraploid plant. In studying the embryos produced on the tetraploid plant it was found that they were triploid. Of fifty embryos studied, thirty had a chromosome number of 13 and twenty had a chromosome number of 14. The embryos with 14 chromosomes apparently arose from the union of diploid pollen grains with haploid egg cells containing five chromosomes. Similarly the embryos with 13 chromosomes probably resulted from the union of diploid pollen grains with haploid egg cells containing four chromosomes.

In studying embryo development in this tetraploid plant it was found that some of the seeds were completely devoid of embryos. In many of these the primary endosperm nucleus increased greatly in size. During this enlargement the chromosomes are in a relic spiral and each terminates in a spherical vacuole (fig. 24). This condition persisted and was found in the mature, but inviable, seeds. In the early stages of primary endosperm nuclear enlargement the vacuoles stain with hematoxylin (fig. 24) while in later stages they fail to do so (fig. 25). Figure 26 is a photomicrograph of a cross section of an embryo sac through the enlarged primary endosperm nucleus. While this enlargement is in progress, the nutritive layer, usually one cell layer in thickness, becomes multilayered (fig. 26). In some embryo sacs the growth of the nutritive layer was so extensive that the embryo sac cavity was no longer evident. In these, the zygote or egg cell and the primary endosperm nucleus or fusion polar nucleus and antipodal cells were crushed. In other cases, there is some evidence of the embryo sac, but the contained cells are crushed or disintegrate (fig. 27).

In other embryo sacs apparently single fertilization rather than double

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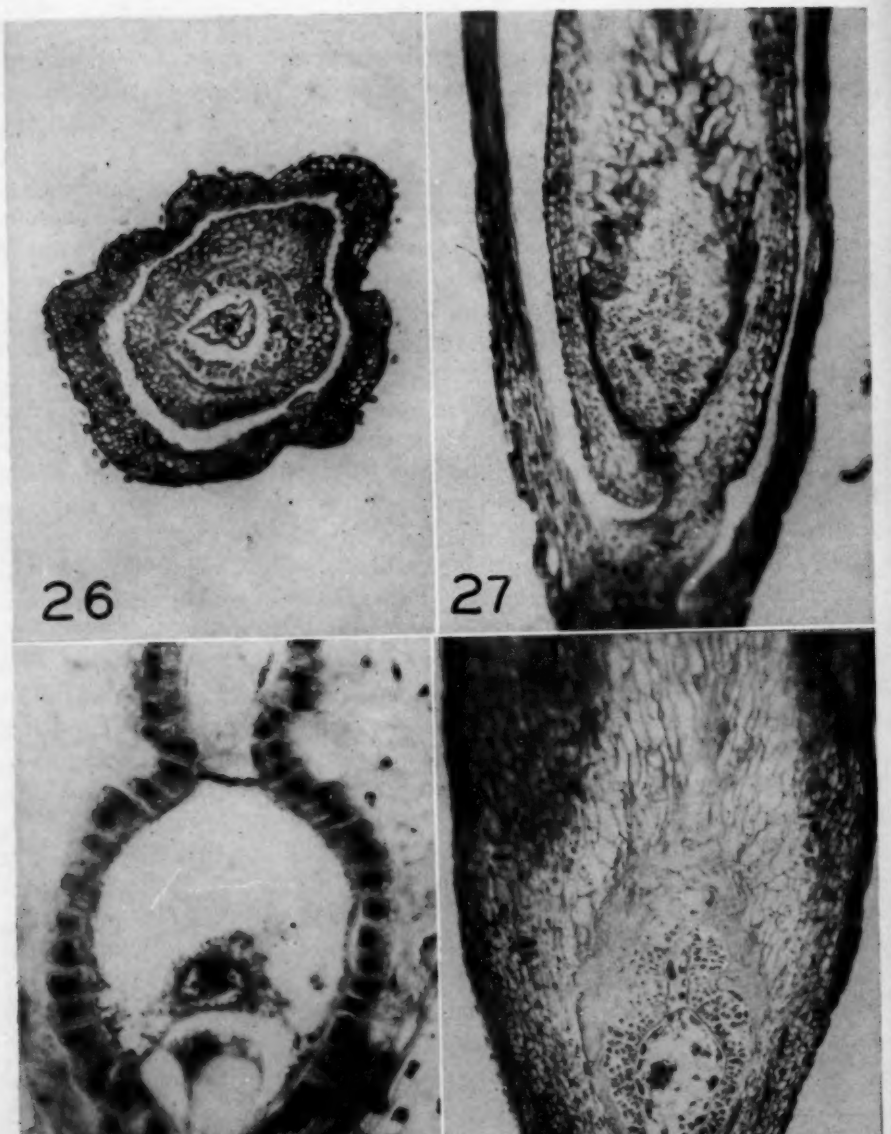
FIGS. 16–23. Photomicrographs of aceto-orcein smear preparations of microsporocytes and somatic cells in various stages of division. Magnification ×1500. FIG. 16. The supernumeraries as three univalents. FIG. 17. Seven bivalents and 1 quadrivalent. FIG. 18. Five bivalents and 2 quadrivalents. FIG. 19. Three bivalents and 3 quadrivalents. FIG. 20. Four quadrivalents and 1 bivalent. FIG. 21. Six bivalents, 1 quadrivalent and 2 univalents. FIG. 22. Metaphase from an adventitious root showing 16 chromosomes. FIG. 23. Metaphase from an adventitious root showing 8 chromosomes. FIGS. 24 & 25. Photomicrographs of iron alum hematoxylin stained sections of embryo sacs of the tetraploid plant. Magnification ×1500. FIG. 24. Enlarging primary endosperm nucleus. FIG. 25. Very much enlarged primary endosperm nucleus.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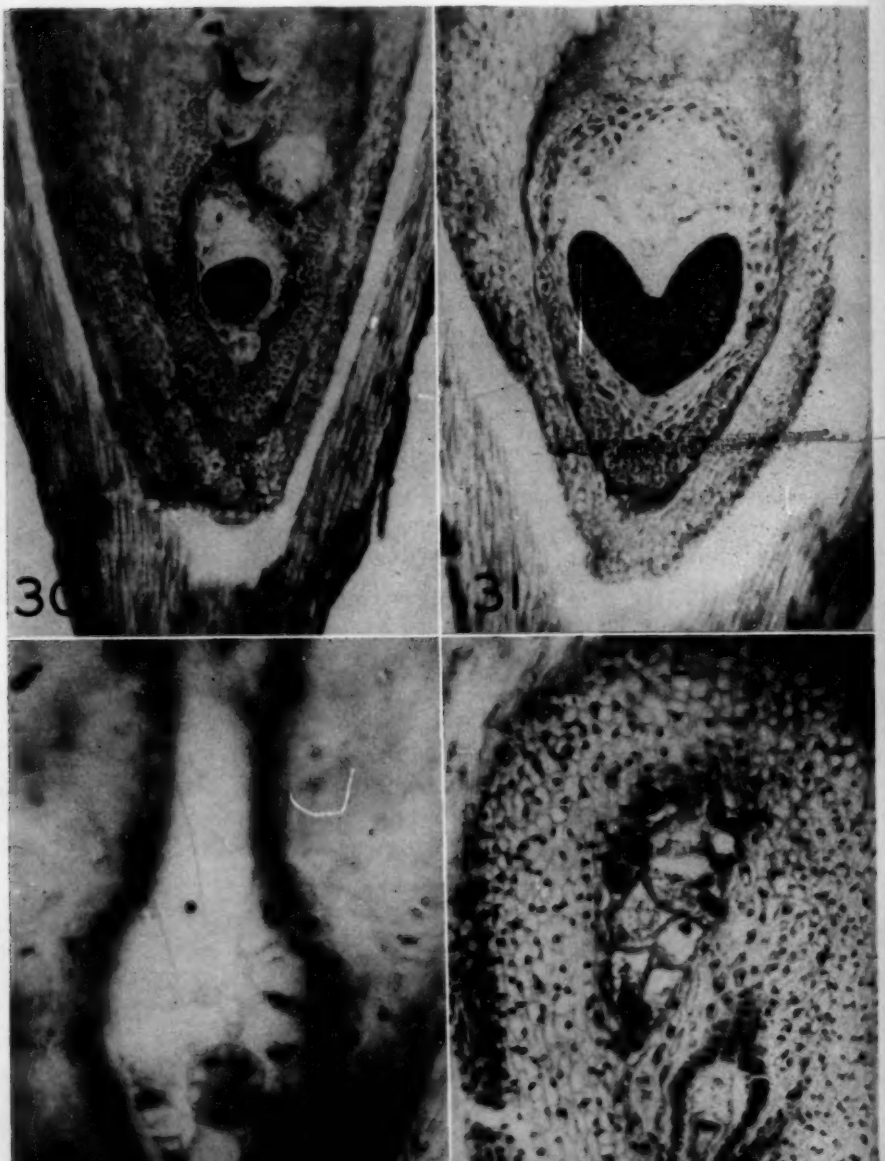
fertilization had occurred, only the egg cell being fertilized. The growth of the embryo was never extensive in such cases. This type of development was also accompanied by an excessive growth of the nutritive layer. The fusion polar nucleus again increased greatly in size and showed the same abnormalities as described above.

In a great majority of the embryo sacs double fertilization occurred (fig. 28) and both the zygote and the primary endosperm nucleus underwent successive mitotic divisions. Although these divisions were normal they were always accompanied by an excessive growth of the nutritive layer (figs. 29 to 31). The growth of the nutritive layer may or may not occlude the chalazal pocket of the embryo sac. In any case the embryos fail to complete normal development. In some embryo sacs the embryo may become quite advanced while enclosed by a single layer of nutritive cells. This nutritive layer completely encircles the whole embryo. This is unlike the nutritive layer in the normal embryo sac which remains open at the chalazal pocket (fig. 32). The age of the embryo at the time of disintegration varied in the different embryo sacs. Compare figures 29 and 31. The embryo in figure 29 is a 16-celled embryo and is undergoing disintegration.

In one very interesting ovary of this tetraploid plant, a tumor was noted outside the embryo sac (fig. 33). The tumor consisted of a mass of very large cells derived from the integumentary cells. The normal integumentary cells in this region are highly vacuolated with a nucleus flattened against the cell wall. In the tumor the cells have increased greatly in size. The cell walls are more heavily thickened than those of the normal integumentary cells. The cell walls are unevenly thickened, resembling in this respect xylem vessels. Unlike the normal integumentary cells, these cells are filled with dense cytoplasm and the large nucleus is centrally located (fig. 34). The nuclei have many nucleoli. The development of this tumor could not be studied, since this was the only case noted.

Discussion. Of the many reported cases of supernumerary chromosomes, a few have many points of similarity with the supernumeraries of *Xanthisma*. In no instance, however, was the behavior identical with *Xanthisma* in all respects. The case most similar to *Xanthisma* was reported in 1940 by Janaki-Ammal. This investigator found supernumerary chromosomes in *Sorghum purpureo-sericeum*. Forty out of 100 plants studied had these additional chromosomes. Twelve plants had one supernumerary, 20

FIGS. 26–29. Photomicrographs of iron alum hematoxylin stained sections of embryo sacs of the tetraploid plant. FIG. 26. Cross section showing enlarged primary endosperm nucleus and multilayered nutritive tissue. Magnification ×100. FIG. 27. Longitudinal section showing excessive growth of the nutritive tissue. Magnification ×100. FIG. 28. Longitudinal section of embryo sac shortly after fertilization. Magnification ×400. FIG. 29. Longitudinal section of embryo sac showing excessive growth of nutritive layer and disintegrating embryo. Magnification ×100.


30
31
32
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had two, 5 had three, 1 had four, 1 had five and 1 had six. On examining the root tips of 20 plants belonging to these different groups no supernumerary chromosomes were found. It was suggested that the supernumerary chromosomes must be lost in the early growth of the roots. Darlington and Thomas (1941) studied the same plant and found that the supernumerary chromosomes were heterochromatic and varied in structure within and between plants owing to frequent spontaneous changes including a misdivision of the centromere. This is unlike the condition found in *Xanthisma* in which case all the supernumerary chromosomes are the same and are not heterochromatic. According to Darlington and Thomas the supernumerary chromosomes in *Sorghum purpureo-sericeum* are sex limited. They are lost in the radicle before seed ripening and in the shoot tissues as they reach maturity. Only in the anthers and ovaries are they regularly maintained. This again is in contrast to the condition as existing in *Xanthisma*. In *Sorghum purpureo-sericeum* the pollen grain divisions in plants containing the supernumerary chromosomes were abnormal. In these divisions the supernumerary chromosomes always passed to the generative pole undivided, thus increasing the number of such chromosomes in the generative nucleus. The vegetative nucleus undergoes extra divisions with the extra chromosomes always going to the generative pole. The extra divisions are malignant and result in the death of the pollen grains. In *Xanthisma* the pollen grain divisions in all plant types were normal.

Lewis (1951) reported supernumerary chromosomes in natural populations of *Clarkia elegans*. The number of supernumerary chromosomes varied from one to six and their meiotic behavior was constant within any given plant. Pairing behavior in *Clarkia* indicates that there are at least two non-homologous supernumeraries; when one of each is present they remain unpaired during meiosis. When two homologous supernumeraries are present they pair normally and behave as members of the basic set. In *Xanthisma* the supernumeraries are all homologous.

The type of sterility found in the tetraploid plant of *Xanthisma texanum* was reported by Brink and Cooper (1939) in *Medicago sativa*, following inbreeding. This type of sterility was termed somatoplastic sterility by these authors and results from excessive growth of the nucellus and impaired growth of the endosperm followed by embryo collapse. Cooper and Brink (1940) reported somatoplastic sterility following a cross between *Nicotiana rustica* and *Nicotiana glutinosa*. Sansome, Satina and Blakeslee

FIGS. 30–33. Photomicrographs of iron alum hematoxylin stained sections of embryo sacs. FIG. 30. Embryo sac of the tetraploid plant containing young embryo surrounded by multilayered nutritive tissue. Magnification ×100. FIG. 31. Later stage in embryo development. Magnification ×100. FIG. 32. Young embryo of a diploid type plant. Note single layered nutritive tissue. Magnification ×400. FIG. 33. Ovary showing tumor outside the embryo sac of the tetraploid plant. Magnification ×200.

(1942) reported seed failure in *Datura stramonium* after 4n × 2n crosses in which the 4n plant represented the female parent. These authors noted that the disintegration of the embryo was accompanied or preceded by the enlargement of the endothelial cells. These cells then divide actively in a plane tangential to the embryo sac as well as radially, so that the endothelium becomes multi-layered and sometimes entirely fills up the embryo-sac. Sometime, however, the endothelial cells disintegrate at the same time as or soon after the embryo sac contents. In the case of the tetraploid plant of *Xanthisma texanum* an overgrowth of the maternal somatic tissue was noted. Sansome, Satina and Blakeslee (1942) suggested that a chromosomal unbalance might be responsible for somatoplastic sterility. In an embryo sac having the normal type of embryo sac development the chromosomal ratio of embryo to endosperm to somatic tissue is 2 : 3 : 2. Any deviation from this ratio may lead to post-fertilization failure. In the tetraploid plant of *Xanthisma texanum* the ratio is 3 : 4 : 2.

SUMMARY

1. Four new chromosomal types of *Xanthisma texanum* were found. Three of these types contained one, three and four supernumeraries respectively. The fourth was a tetraploid with two supernumeraries.

2. Microsporogenesis in these types is described.

3. The sterility of the tetraploid was studied and found to be due to "somatoplastic sterility."

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THE CYTOLOGY OF XANTHISMA TEXANUM D. C. III. DIFFERENTIAL SOMATIC REDUCTION[1]

C. A. BERGER, R. M. MCMAHON & E. R. WITKUS

Earlier cytological studies of the composite, *Xanthisma texanum*, (Berger & Witkus 1954, Witkus, Lowery & Berger 1955) showed that many plants of this species have a higher number of chromosomes in the cells of the shoot than in those of the root. Root cells of all plants have a diploid chromosome number of 8. Shoots of different plants have chromosme numbers of 8, 9, 10, 11 and 12. In any individual plant the chromosome number of the shoot is highly constant for all the cells and is found in germ as well as in somatic cells. Numbers higher than 8 are due to a small supernumerary chromosome, chromosome V, of which one, two, three or four may be present in the shoot cells of different plants.

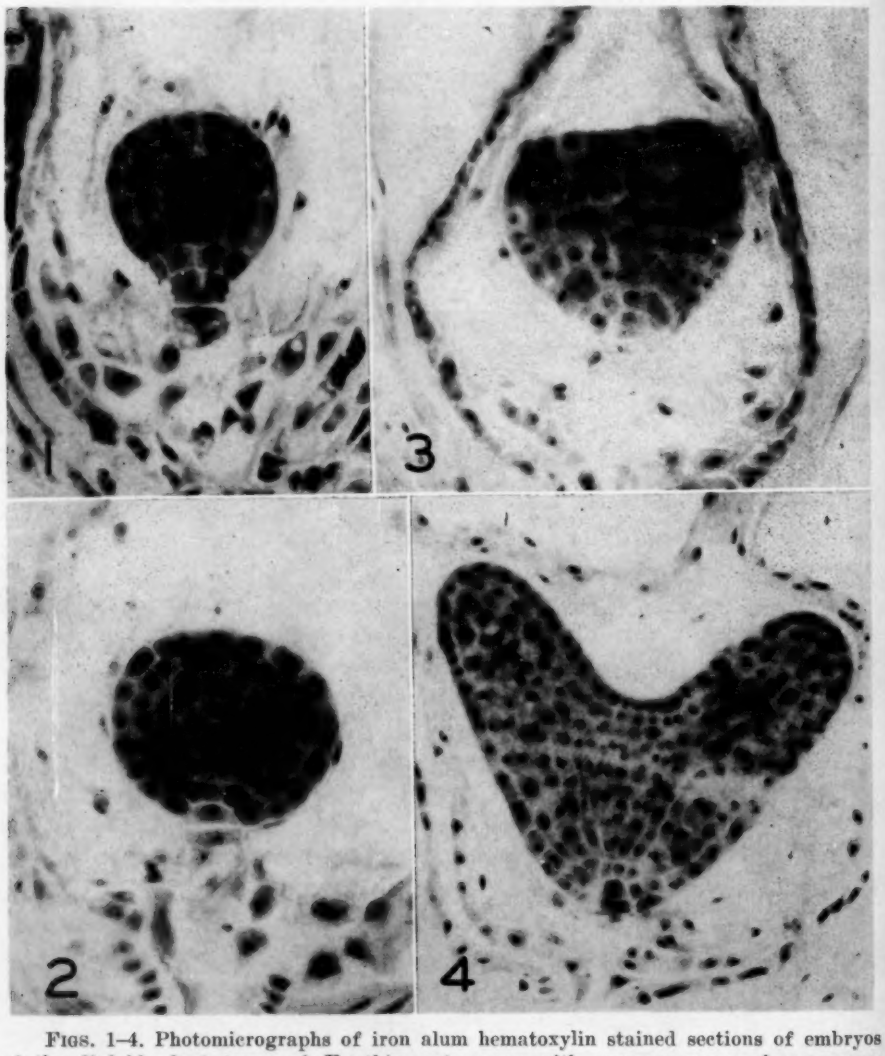
Since root cells never contain supernumerary chromosomes, it is obvious that they must be lost early in development. The supernumerary chromosomes of *Xanthisma* differ from most other reported cases of supernumeraries in that they are retained in the shoot but eliminated from the roots. This difference indicates a possible relation between the change in chromosome number and the differentiation of root and shoot tissue. The embryos of all plants having one or more supernumeraries likewise contain one or more of these extra chromosomes. In such embryos the differentiation of root tissue is accompanied by an elimination of the supernumerary chromosomes. This is a clear case of somatic reduction and one that is correlated with the differentiation of fundamental tissues. For the above reasons it was decided to investigate the early embryology of *Xanthisma* to ascertain when and by what means this reduction in chromosome number occurs.

Materials and methods. Inflorescences from all types of plants were fixed in Craf fixative after a ten minute pretreatment with Carnoy's solution. Individual flowers were dissected out in 70% alcohol and imbedded separately. Longitudinal and cross sections were cut at 10 microns and stained in iron-alum hematoxylin and by the Feulgen technique. Acetoorcein smear preparations were also made.

Observations. The early divisions of the zygote showed the number of chromosomes characteristic of the shoot, i.e. the unreduced number, including the supernumeraries. This condition continued through the early spher-

[1] This investigation was aided by a Grant (G1149) from the National Science Foundation.

ical-embryo stage (fig. 1). In the late spherical-embryo stage (fig. 2), the first indication of reduction was seen in the presence of micronuclei in a few of the cells at the basal end. When the embryo attained the early heart-



FIGS. 1–4. Photomicrographs of iron alum hematoxylin stained sections of embryos of the diploid plant types of *Xanthisma texanum* with supernumerary chromosomes. Magnification × 400. FIG. 1. Young spherical embryo taken from a plant of the 5 bivalent and 1 univalent type. FIG. 2. Slightly older spherical embryo of the 4 bivalent and 1 univalent type. An occasional micronucleus is visible in the basal portion of the embryo. FIG. 3. Young heart-shaped embryo taken from the same plant as figure 2. Micronuclei are very abundant in the basal portion of the embryo and not evident in the apical region. FIG. 4. Older heart-shaped embryo from a 4 bivalent and 1 univalent type plant.

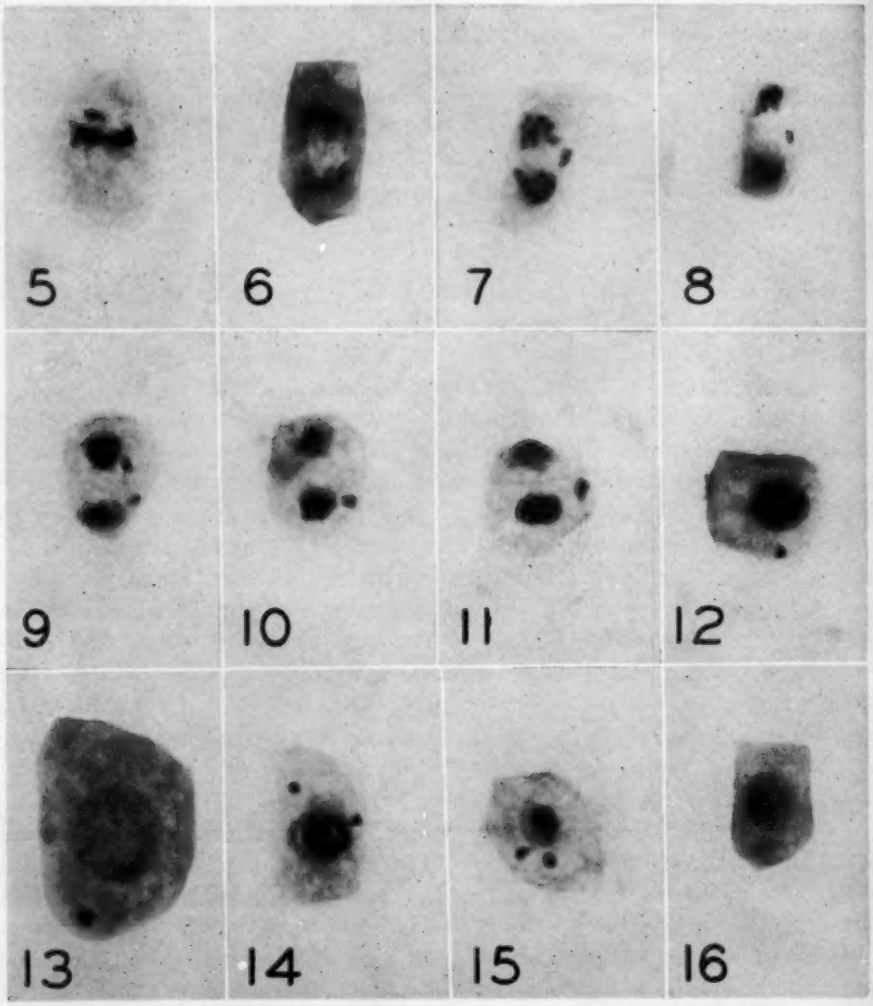
shaped stage (fig. 3), micronuclei were found in the cytoplasm of many of the cells at the basal end. This condition continued into the late heart-shaped embryo (fig. 4). At this stage many of the cells in the basal, root-forming region had micronuclei present, while they are rare or absent in the young cotyledon and shoot tissue.

A study of mitotic divisions during the transition from late-spherical to heart-shaped embryos revealed the mechanism by which the elimination is accomplished. The supernumeraries may fail to congress on the metaphase plate (fig. 5). At anaphase lagging of the supernumeraries is very common (figs. 6 to 9). They are left in the cytoplasm where they may persist for several division cycles as micronuclei (figs. 10 to 16). These micronuclei are Feulgen positive.

Discussion. Cases of different chromosome numbers in root tips and in pollen mother cells had previously been found in *Sorghum purpureo-sericeum* (Janaki-Ammal 1940 and Darlington and Thomas 1941) and in *Poa alpina* (Müntzing 1946, 1948 and Hakansson 1948). Janaki-Ammal (1940) and Darlington and Thomas (1941) thought that the accessory chromosomes were lost in somatic tissue and restricted to the germ line. In the twenty plants studied by Janaki-Ammal no B-chromosomes were found in the root tips. The author suggested that the B-chromosomes were lost in early root development. Darlington and Thomas (1941) reported the absence of B-chromosomes in the roots of plants with varying numbers of B-chromosomes. Since no B's were found in the youngest root tips from seeds it was suggested by these authors that the chromosomes were lost in the early embryology of the plant. The chromosomes were also lost in the shoot and were retained only in the so-called germ line. Loss was attributed to an inadequacy of the centromere, delayed congression on the metaphase plate and lagging at anaphase with the resultant formation of micronuclei which were lost in the cytoplasm.

Müntzing (1946 and 1948) in a study of 300 plants of *Poa alpina* found the B-chromosomes lacking in the roots of potted plants. An occasional cell with B-chromosomes was found in the root tips. Müntzing did not determine the time and place of elimination of the B-chromosomes. Hakansson (1948) studied the early embryology of *Poa alpina* to ascertain the time and manner of elimination of the B-chromosomes. Hakansson (1948) found that elimination of B-chromosomes was rare in developing embryos. Division stages in all parts of the embryo as a rule showed more than fourteen chromosomes. Only in the primary root of nearly mature embryos was there evidence of a more frequent elimination of B-chromosomes. Since no evidence of elimination was found in the embryos, primary roots from germinating seeds were investigated. These roots also had many B-chromosomes. This observation of Hakansson is in disagreement with the earlier obser-

vation of Müntzing that B-chromosomes were lacking in the roots of young seedlings. As suggested by Hakansson, this discrepancy may be explained by assuming that Müntzing studied adventitious roots while Hakansson



FIGS. 5–16. Photomicrographs of cells taken from iron alum hematoxylin stained sections of embryos of *Xanthisma texanum* (Types with supernumerary chromosomes). Magnification ×1500. FIG. 5. Metaphase plate showing failure of congression on the plate. FIGS. 6 to 11. Various mitotic stages showing lagging of the supernumerary chromosomes. FIGS. 12–16. Cells showing micronuclei in the cytoplasm.

used primary roots. It was also suggested by Hakansson that elimination occurs in the first divisions of the pericycle cells in the formation of adventitious roots.

The tendency to mitotic elimination of supernumerary chromosomes in *Xanthisma* is similar to that occurring in *Soghum purpureo-sericeum*. The youngest roots of germinating seeds of *Sorghum* and *Xanthisma* have no supernumerary chromosomes. In both cases the supernumeraries have been lost during seed development. In *Sorghum purpureo-sericeum* the exact time and place of this elimination was not determined. In *Xanthisma texanum* it occurs when root and shoot tissues are differentiated in the late spherical stage of the embryo. In young shoots of *Sorghum* a loss sometimes occurs. As the shoot matures the rate of loss is increased. Inflorescences, filaments and glumes are littered with micronuclei while there is no elimination in parts that are going to produce germ cells. The anther walls and ovaries show an intermediate loss. They have rare micronuclei. The loss of B-chromosomes in different tissues of *Sorghum* during development has been attributed to a variation in the activity of the spindle. In *Xanthisma texanum* the supernumerary chromosomes were regularly maintained in the shoot. When adventitious roots of cuttings were studied they were found to have the supernumerary chromosomes indicating a retention of such chromosomes in older tissues of the shoot.

Since the supernumerary chromosomes of *Xanthisma* have a perfectly normal mitotic behavior in the shoot, it cannot be said that their centromeres are defective.

Apparently the differentiation of root tissue in early embryology involves some factor or condition that makes it difficult or impossible for the supernumeraries to react normally with the spindle.

SUMMARY

1. Supernumerary chromosomes are present in all the cells of the young embryo up to the late spherical stage.

2. At the transition from the late spherical stage to the heart-shaped embryo root and shoot tissues are differentiated.

3. In the cells of the root tissue the supernumerary chromosomes are eliminated and are seen as micronuclei in the cytoplasm.

4. Elimination is brought about by lagging of the supernumeraries at mitosis.

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A CONSIDERATION OF A NEW TYPE OF MEIOSIS (MIS-MEIOSIS) IN JUNCACEAE (LUZULA) AND HEMIPTERA

EMILIO BATTAGLIA[1, 2]

Some years ago (1945, 1950) the present author discussed most known types of meiosis and proposed an appropriate terminology for the different cases. More recently new exceptional meiotic chromosome mechanisms have been reported in the cytological literature, namely for *Luzula* (Juncaceae) by Noronha-Wagner and Castro (1952b) and for Hemiptera by Piza de Toledo (1946a, 1946c, 1946e, 1947e, 1950, 1953), and by Piza and Zamith (1946). In both cases a similar type of meiosis has been described, characterized by the apparent transverse breakage of chromosomes at first and second anaphases. This new chromosome mechanism of meiosis will be here critically reviewed.

Luzula campestris and L. nemorosa. The chromosomes of the genus *Luzula* are usually considered to possess the so-called "diffuse centromere" or "diffuse kinetocore." At present there is a lack of uniformity of opinion regarding chromosomes with this type of centromere. Some cytologists consider them to be polycentric (Rhoades & Kerr 1949, La Cour 1953, Godward 1954a, 1954b) while Piza (1939a–1953) believes them to be dicentric having two terminal centromeres. On the other hand, most authors believe that the chromosomes of these plants have a diffuse kinetocore (Hughes-Schrader & Ris 1941; Ris 1942; Brieger & Graner 1943; Federley 1943, 1945; Schrader 1947; Lima-de-Faria 1949; Östergren 1949; Brown 1950, 1954; Nordenskiöld 1951; Helenius 1952; Suomalainen 1953). Others hold that they simply lack a localized centromere (Malheiros, Castro & Camara 1947) or that they completely lack a centromere (Castro 1950). The present writer prefers the terminology "multiple spindle attachments" or "diffuse spindle attachments," since the number and position of the spindle fiber attachments seem indefinite and perhaps variable.

Meiosis in *Luzula purpurea* follows the post-reductional type of meiosis, as was clearly demonstrated by Malheiros, Castro and Camara (1947), and later confirmed by Berger (1949) and La Cour (1953). Other species of this genus have also been found to possess the post-reductional type of meiosis (*Luzula campestris*: Gardé and Malheiros-Gardé 1953; and *Luzula*

[1] The author wishes to acknowledge his indebtedness to Dr. C. A. Berger for his criticism and assistance.

[2] Center of study of plant cytogenetics of the National Council of Research, Florence, Italy. Publication number 190.

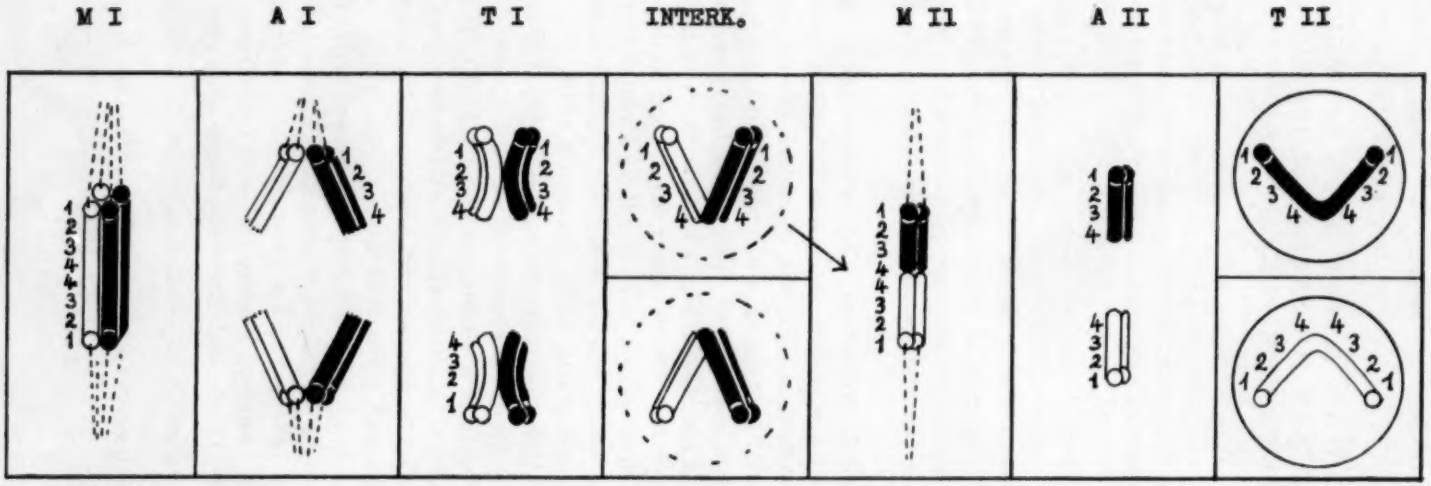

FIG. 1. Schematic outline of *mis-meiosis* according to the interpretation of Piza de Toledo (see text). The effects of crossing-over have been omitted to avoid unnecessary complication in discussing the chromosomes. The meiotic chromosome mechanism is illustrated in one bivalent. One homologue (2 chromatids) of the bivalent has been drawn in black, the other one in white. The small circle at each chromosome end represents a "terminal centromere." Thus the chromosomes are seen to be dicentric (in the sense of Piza de Toledo). The numbers 1, 2, 3, etc. indicate the hypothetical sequence of chromosome loci, to clearly indicate the assumed "isochromosome structure" of some of the chromosomes. Chromosomal fibers have been connected only to the centromeres, but according to a recent suggestion (Piza de Toledo 1950) they are spread out along the surface of the whole chromosome (see text).

silvatica: Michalska 1953). In contrast to the above reports, Noronha-Wagner and Castro (1952b) have claimed that in *Luzula campestris* and *L. nemorosa* the course of meiosis is as follows:

During M I-A I bivalents place themselves perpendicular to the equatorial plate. At the beginning of A I the four chromatids of each bivalent are pulled to the poles by opposed centromeric forces that seem to be located at their two ends. In this way they are stretched until they are forced to break in the middle. Following this rupture the 24 hemi-chromatids of each telophasic nucleus fuse two by two reconstituting 12 chromosomes. At second division the chromosomes undergo pairing again and at A II they behave as at first division, the only difference being that now reduction takes place after hemi-chromatid fusion. . . .

Noronha-Wagner & Castro (1952b) think that only isochromosomes lacking a localized centromere can behave in such a way and, moreover, suppose that it is the consequence of pairing between the two identical halves of the same iso-chromosome (Noronha-Wagner & Castro 1952b, p. 161). This type of meiosis has been diagrammed in figure 2. In this drawing, and in the other figures, the numbers 1, 2, 3, etc. have been introduced to indicate a hypothetical series of loci on the chromosomes. From the numerical order of the loci the assumed isochromosome structure of the bivalents and subsequent changes in structure can clearly be followed. For the sake of simplicity, the possible results of crossing over have been omitted. Considering the similar phenomenon of mis-division, I suggest the term *mis-meiosis* for this unique meiotic chromosome behaviour.

A critical examination of the Noronha-Wagner and Castro report however leads the author to doubt whether mis-meiosis occurs in *Luzula campestris* and *L. nemorosa*. Such a conclusion is based on the following considerations:

a) Metaphase chromosomes are highly spiralized. Their transverse breakage, as postulated in mis-meiosis, should be the last event of a progressive despiralization attaining the crucial point at the middle of the chromosomes. The presence of anaphase bridges would be commonly seen in the last stages of such a division, and chromosome fragments should be a frequent feature of both first and second meiotic divisions. True bridges undoubtedly occur in *Luzula purpurea* (Castro & Mello Sampayo 1953). The bridges of *Luzula campestris* (Noronha-Wagner & Castro 1952b) however are different in number, shape and position, and they seem to be the consequence of a high degree of chromosome stickiness. In other words, in the writer's opinion, the bridges of *Luzula campestris* are a connection of the chromosome matrix (matrix connections) instead of true bridges. The irregularity and thinness of these bridges and also the presence of one or more blocks of chromosomal material in the middle region of the bridges

fig. 2

FIG. 2. Mis-meiosis according to the interpretation of Noronha-Wagner and Castro (1952b). Here also the bivalent under consideration has the isochromosome structure, but instead of two terminal centromeres a diffuse kinetochore is assumed (see also explanation of fig. 1).

(Noronha-Wagner & Castro 1952, figs. 1 and 2) strongly support the above interpretation. Noronha-Wagner and Castro consider such blocks as "una retenção de substancia matriz."

b) The last named authors have also described meiosis in a plant of *Luzula campestris* showing one supernumerary heterochromatic chromosome (Noronha-Wagner & Castro 1952a). According to their report, at meiosis I, this accessory chromosome appears as a heterochromatic univalent and divides synchronously with the bivalents at anaphase. Chromosome behaviour during meiosis II was not studied for lack of material. However it has been observed that only two of the four microspore nuclei showed a heterochromatic chromosome.

The meiotic behaviour of this supernumerary heterochromatic chromosome seems to show that mis-meiosis does not occur. Since only two of the four microspore nuclei possess one heterochromatic chromosome, the indication is that each half of a univalent (that is the unit in movement at anaphase I) has not divided at anaphase II, and has been included in only one of the two nuclei of telophase II. On the contrary the writer thinks that the behaviour of univalents during a true mis-meiosis would be different and their derivatives distributed to all four spore nuclei (microspores) instead of two. A univalent (two sister chromatids) having the length U (unity) should distribute to each pole one pair of sister chromatids of length U/2. This would result from a broken univalent of length U. During interkinesis, or later, as a result of the fusion of the broken ends, one isochromosome of length U should arise, similar in size and shape to the isochromosomes produced by each half of the bivalents (two isochromosomes from each half of the bivalent). At anaphase II, such isochromosomes (having length U, as the other isochromosomes) will again undergo transverse breakage and consequently all telophase II nuclei will have chromosome derivatives of U/2 length. However the derivatives from bivalents will be able to restore the isochromosome structure by fusion of the broken ends, since they occur in pairs. On the contrary, derivatives of univalents should persist as a chromosome body of halved length (U/2).

From the above considerations it is concluded that mis-meiosis probably does not occur in *Luzula campestris* and *L. nemorosa*. In this connection it may be mentioned that Malheiros-Gardé and Gardé (1951, p. 171) examined the preparations of Noronha-Wagner and Castro and deduced that the post-reductional type of meiosis occurs in *Luzula campestris*. The same interpretation has also been suggested by the above cited authors (Gardé and Malheiros-Gardé 1953, p. 118–119) for meiosis in trisomic plants of *Luzula campestris*. In these plants (cf. also Noronha-Wagner and Castro 1952a, 1952b) a supernumerary heterochromatic univalent was found to divide at anaphase I and its derivatives passively distributed at anaphase

II, without division. More recently, Brown (1954) has also described meiosis in *Luzula campestris*. His description differs in that he considers the course of meiosis to be quite normal, that is according to the prereductional type of meiosis (prereduction). Noronha-Wagner and Castro (1952b) also report that their interpretation of meiosis in *Luzula campestris* and *L. nemorosa* was similar to the interpretation given by Piza (1946c) for meiosis in *Corizus hyalinus* (Hemiptera). This question will be discussed in more detail later.

Hemiptera. Piza (1946a, 1946b, 1946c, 1953) described a form of mismeiosis in Hemiptera similar to that reported by Noronha-Wagner and Castro except that in the Hemiptera studied the chromosomes are considered to have a terminal centromere at both ends and the isochromosome structure. According to Piza's scheme (1946c, fig. 7; 1953, figs. 16–22, 29, 30) isochromosome dicentric bivalents undergo transverse division in the median region. (According to the writer's opinion a more exact phrase than "transverse division" would be "transverse breakage.") The unit in anaphasic movement (A I) is a V-shaped chromosome complex with centromeres at the vertex. From the end of the first division to the metaphase of the second, the centromeres occupying the vertex of the V go apart from one another, making the chiasmata existing there slip to opposite extremities, and thus changing the V into an X. When the chiasmata reach the acentric ends, the X is again converted into a V. The V of the second metaphase, therefore, differs from the V of the first anaphase, in being inverted, that is, in having the centromeres in the extremity of its arms, and no longer in the vertex as in the latter (Piza 1953, p. 183).

In figure 1, for easier comparison with figure 2, the chromosome unit of metaphase II has been drawn in the shape it assumes immediately before anaphase, that is, with "I" shape instead of "X" or "V." Obviously the units of anaphase movement (A II) must later restore their dicentricity: "Dicentricity of the chromosomes is ascribed to the division of the kinetochore of the chromosomes reaching the poles followed by separation and distention of the chromatids which remain fused at the acentric ends giving thus origin to terminally dicentric isochromosomes." (Piza 1946a, p. 51.) The type of meiosis outlined in figure 1 is considered by Piza de Toledo as the general case of autosome behaviour for Hemiptera. Such a type would also occur in the species of *Luzula* investigated by Noronha-Wagner and Castro (1952a and b). It should be mentioned that Piza de Toledo considers practically all the examples of diffuse centromeres in the current literature as actually dicentric. From an examination of the text and figures of Piza de Toledo, the following five objections to the occurrence of mismeiosis may be given:

1) Lack of morphological evidence of chromosomal stretching to support

the idea of their transverse breakage. (see criticism of the first case of mismeiosis.)

2) Failure to explain the general occurrence of an evident constriction at the breakage point, clearly visible at metaphase I.

3) Lack of any proof of the abnormal persistence and behaviour of chiasmata between telophase I and metaphase II;

4) Lack of evidence of the duplicity of chromosomes at anaphase II;

5) Lack of evidence of the process restoring the isochromosome structures at the end of meiosis. In such a case the behaviour of the broken ends would be in conflict with the present knowledge of healing of broken chromosome ends. Another similar observation might also be pointed out concerning the behaviour of the centromere.

It is evident from Piza de Toledo's paper that he considers both mismeiosis and dicentricity as phenomena of general occurrence for the organisms now known to have both regular meiosis (pre-reductional or post-reductional meiosis) and diffuse kinetochores. (*Tityus bahiensis* is an exception in that it shows a regular meiosis, cf. Piza de Toledo 1939a, 1940, 1950, 1953). It is clear that dicentricity in the classical sense of the presence of two normal centromeres, is not the case in *Luzula purpurea*, so carefully investigated by Malheiros, Castro and Camara (1947) and later confirmed by Berger (1949) and La Cour (1953). However in a recent paper Piza de Toledo (1950, p. 195–196) discusses precisely what he considers as a centromere, including its physiological peculiarities. This will be discussed further.

Chromosome dicentricity and bending. The Feulgen and oxyquinoline aceto-orcein techniques (Tjio and Levan 1950a, b) are well known cytological methods for demonstrating the centromeres. As far as the author knows, neither of these methods has been used by Piza de Toledo to determine the presence of terminal centromeres. On the contrary his essential proof of dicentricity has been the curving of anaphase chromosomes with both ends turned towards the corresponding pole.

Assuming that spindle fibers are "traction fibers" (Cooper 1941; Cornman 1944, 1951; Hughes and Swann 1948; Ris 1949; Schrader 1953), it naturally follows that chromosome bending is a result of chromosome flexibility and deformability. From this point of view anaphase I chromosomes having two-chromatids should be less flexible than chromosomes of anaphase II, which consist of one chromatid. Hughes-Schrader and Ris (1941) investigating the coccid *Steatococcus tuberculatus* observed at meiosis I that "as the chromosomes approach the pole some bending of their ends toward the centriole occurs, . . . but this clearly involves no special locus; it seems rather to reflect the effect of pressure on the whole chromosome from the narrowing space of the polar cones" (Hughes-Schrader and Ris

1941, p. 434). This is in agreement with the author's point of view.

However it is also clear that the chromosomal curvature will reach its maximum at the completion of anaphase since the spindle fibers have exerted their traction forces. Rhoades and Kerr (1949) investigating the behaviour of chromosome fragments induced in males of *Tityus* by X-ray treatments, have written concerning chromosome curving: "the turning of the ends towards the poles may be nothing more than an adaptation permitting the chromosomes (huge compared to cell size) to converge to the spindle poles and they may be polycentric" (Rhoades and Kerr 1949, p. 131). This explanation does not differ substantially from that offered by Hughes-Schrader and Ris (1941).

In all cases of the so called diffuse kinetochore the spindle fibers are spread with uniformity over the chromosome surface. As a result the numbers of spindle fibers should be a function of the surface of the chromosome. However it is evident that the extremities of the chromosome possess more surface than non-terminable parts having the same length. Thus in cases of diffuse centromere both the chromosome ends might show a greater number of spindle fibers than elsewhere. Therefore the ends might be subjected to greater traction than the rest of the chromosome, and as a result the chromosome would assume the curved form described above.

The dicentricity emphasized by Piza de Toledo, cannot be understood in the classical sense. He has clarified this point in a recent paper:

"The idea of a spindle organizing substance escaping from the centromere was exactly that which occurred to me in one of the first attempts to interpret the nature of the spindle (Piza 1939a, 1943a). The possible existence of an active substance along the whole body of the chromosomes as admitted by Castro, Camara and Malheiros (1949) constituted the ground for an explanation I proposed for the presence of interjacent fibres in the polar side of *Tityus* chromosomes (Piza 1946). The sole difference between the point of view of the Portuguese investigators and my own is that the former consider the fibre producing substance as originating from the body of the chromosomes, while in my opinion and for the case of *Tityus,* this substance, coming out from localized points (the centromeres), flows along the chromosome body" (Piza de Toledo 1950b, pp. 195–196).

According to this interpretation it is evident that the dicentric chromosomes of Piza de Toledo and chromosomes with the diffuse kinetochore both show spindle fibers attached to the entire body. It follows then that the question of curved ends discussed above loses any significance as a differentiation between dicentric and diffuse kinetochore chromosomes. The dicentricity assumed by Piza de Toledo is substantially based on a new type of centromere. It is a centromere having the peculiar property of producing a spindle organizing substance that flows along all the chromosome body.

(For a criticism of Piza de Toledo's hypothetical spindle organizing substance, see Schrader 1947, pp. 141–142; and Östergren 1949). Starting from this supposition even only one centromere could give rise to the condition of "diffuse centromere" (diffuse spindle fiber attachments). All the above considerations lead to the conclusion that at least for the present time the Piza de Toledo interpretation of dicentricity cannot be accepted.

Consequences of mis-meiosis. The perpetuation of chromosome fragments is the most important property of organisms having a diffuse kinetochore. Bridges, fragments, chromosomal races or better karyological biotypes characterized by different numbers have been observed in *Luzula purpurea* (Castro and Mello-Sampayo 1953). The multiple chromosome numbers observed in this genus (*agmatoploidy:* Malheiros-Gardé and Gardé 1950, 1951; *endo-nuclear polyploidy:* Nordenskiöld 1951; *pseudopolyploidy:* Battaglia 1955b) also seem to be a result of the fragmentation phenomena. It is surprising to note that both *Luzula purpurea* and *Tityus bahiensis* have the same somatic, or better, *zygotic number* $z = 6$ (Battaglia 1955a). Also as in the genus *Luzula*, *Tityus* shows karyological races (2n: 7, 8, 9, 10; cf. Piza de Toledo 1947a, *c*, 1948a, *b*, c) and karyotypes characterized by different number and by chromosomes having different sizes (*Tityus serrulatus* 2n: 12: Piza de Toledo 1947a, p. 173; *Tityus trivittatus*, 2n: 14: Piza de Toledo 1948a; *Tityus mattogrossensis* 2n: 20: Piza de Toledo 1947a, etc.). In this respect, the genus *Tityus* resembles *Carex* and other genera of Cyperaceae where fragmentation is believed to be the mechanism for increasing the chromosome number (Malheiros-Gardé and Gardé's agmatoploidy). The condition "diffuse kinetochore" is generally considered to occur in *Luzula* and *Tityus* and perhaps also occurs in all the genera of Juncaceae and Cyperaceae (Castro 1950; Malheiros-Gardé and Gardé 1950, 1951; Nordenskiöld 1951). In the Cyperaceae the diffuse kinetocore, more exactly the "lack of one localized centromere," has been recently observed by Håkansson (1954) and the author (Battaglia 1954), specifically in *Heleocharis palustris* and *H. uniglumis*. In Hemiptera, among animals, and in *Spirogyra*, among algae, the hypothesis of the "diffuse kinetochore" has been accepted by many authors. Even in these organisms the variability of chromosome number suggests the probable occurrence of the phenomenon of pseudopolyploidy (Battaglia 1955b) as a result of chromosome fragmentation. Consequently it seems valid to deduce that chromosome fragmentation plays an important role in the karyotypic evolution of organisms possessing a diffuse kinetochore. The author believes that mis-meiosis does not take place in *Luzula*, Hemiptera, etc. However the hypothetical occurrence of this chromosome mechanism during meiosis must not be disregarded.

Noronha-Wagner and Castro (1952b) pointed out that during anaphase

fig. 3

FIG. 3 represents chromosome mechanisms which may operate during mis-meiosis. It is assumed that the bivalent at metaphase I does not possess an isochromosome structure nor a localized kinetochore (that is, it has a diffuse spindle attachment; see text) (see also explanation of figs. 1 and 2).

II of mis-meiosis the failure of the broken ends to fuse should result in a doubling of the chromosome number. Mis-meiosis however is a peculiar abnormal type of meiosis that theoretically might give rise to several different chromosome structures and numbers (fig. 3). If a normal chromosome structure (not an isochromosome) and a chromosome length equal to U are assumed, then at anaphase I, when fusion of the broken ends occurs, isochromosomes of length U should be produced. On the contrary lack of such fusion should produce normal chromosomes of U/2 length. (This might result in the karyotype change, for instance, from the zygotic number $z = 6U$ to $z = 12U/2$; for z = zygotic number; g = gametic number: Battaglia 1955a). At anaphase II failure of fusion between broken ends might be repeated, producing chromosomes of U/4 length, and a karyotype change from $z = 6U$ to $z = 24U/4$. The karyotypes $z = 6U$, $z = 12U/2$, $z = 24U/4$, $z = 48U8$, have been found in the genus *Luzula* (Nordenskiöld 1951). Irregular karyotypes, that is those having chromosomes of different sizes (U/2, U/4, U/8) and not arithmetically multiple numbers, have also been reported in the genus *Luzula*. The same remarks on the karyotype morphology and the same occurrence of *pseudopolyploidy* might be applied in general to organisms having 'diffuse kinetochores.'' Mis-meiosis would be a meiotic mechanism able to explain such cytological phenomena. However the author believes there is no proof at the present time for the actual occurrence of mis-meiosis in any organism.

The scheme represented in figure 3 is not comprehensive of all possible chromosomal behaviour during mis-meiosis. Thus for example monochromatid isochromosomes produced at telophase I might break at anaphase II, instead of being passively transported to one or the other pole as represented in figure 3. Otherwise, broken sister chromatids might pair, from telophase I to metaphase II, and disjoin at anaphase II, as can be seen in figure 3. The above considerations lead us to the conclusion that although mis-meiosis is at present not demonstrated with certainty in either plants or animals, it may represent a working hypothesis of remarkable interest.

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Fig. 3 represents chromosome mechanisms which may operate during mis-meiosis. It is assumed that the bivalent at metaphase I does not possess an isochromosome structure nor a localized kinetochore (that is, it has a diffuse spindle attachment; see text) (see also explanation of figs. 1 and 2).

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BULLETIN OF THE TORREY BOTANICAL CLUB

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TORREYA

FIELD TRIP REPORTS

April 3. St. John's in the Wilderness. A joint Torrey-Rockland Audubon group attended this annual service (see Torreya in Bull. Torrey Club **81**: 460. 1954). The botanical activities preceding the service were limited because of the rain and they consisted of using live material to test sample the recent WINTER KEY TO WOODY PLANTS by A. H. Graves (reviewed in this issue). Attendance: Torrey 7, Rockland Audubon 7. Leader, J. Harry Lehr.

April 23. Orange County, N. Y. The morning was devoted to such habitats as along a brook, a hillside exposure, and boulder outcroppings. *Aquilegia canadensis* was just coming into flower. The expected associates were seen and listed, 23 flowering species. *Dentaria diphylla* was contrasted with *D. laciniata* which is less common here, blue and white forms of *Hepatica americana* were admired. The lime-loving ferns *Asplenium Ruta-muraria* (*A. cryptolepis* Fern. in Gray's 8th) and *Camptosorus rhizophyllus* were present.

After lunch the plants of the leader's garden were studied with equal profit, highlights being *Amelanchier arborea* approx. 14″ in diam., *Magnolia stellata* fully in flower (it escapes frost here only about every third year), *Claytonia caroliniana* contrasted with *C. virginica*, the Confederate and common *Viola papilionacea*. Attendance 15. Leader, John A. Crabtree.

April 24. Appalachian Trail on Kittatinny Ridge, N. J. The work trip covered about one-half the distance before being called on account of rain. It will be concluded on Oct. 22, please come. Most showy display was shadbush in flower. Attendance 7. Leader, John A. Small.

April 30. Sussex County, N. J. The group stopped at the *Trollius laxus* station in Greendell Swamp, to find it in a profusion of bloom. While engaged in observing this local species, a wedge of Canada geese was seen and heard overhead. Golden club was in bloom and showy orchis in bud near Springdale. *Ricciocarpus* and the edible morel were located near Swartswood Lake. A stand of yellow water-crowfoot (*Ranunculus flabellaris*) was found in a tiny pond near the Sunrise Mtn. Road entrance to Stokes Forest and nearby the previously discovered station of *Trillium erectum* was noted to be increasing in size. Attendance 27. Leader, David Fables.

May 1. Vicinity of Pluckemin, Somerset County, N. J. (See also Bull. Torrey Club **81**: 91–92. 1954). A river terrace forest about 7 feet above the water level of the North Branch of the Raritan River, formerly dominated by oak, is becoming a sugar maple forest. Within the forest are found principally sugar maple, ash, basswood, beech, elm, and hickory. Sugar maple seedlings are very abundant and these grow up into clusters of saplings when an opening occurs in the canopy due to a fallen tree. May-apple is the dominant herb in spring but herbs become sparse during the summer.

Between the terrace and the natural levee bordering the river there is a low, wet inner flood plain which receives much of the force of flood waters. This area is very diversified with respect to habitats and species. No tree species is dominant although sugar maple is abundant on the higher ground between low, wet slough areas. Red maple, river birch, pin oak, swamp white oak, black gum and individuals from the foregoing habitat are found here. Saplings of many species grow where openings appear in the canopy. May-apple does not dominate the entire inner flood plain—the herb cover is more diverse and *Mertensia*, not found on the terrace, is common.

Near the river, on the natural levee, there is a fine mesophytic forest of large trees. Species include: sugar maple, beech, American and slippery elm, tuliptree, ash, hickory, boxelder, sycamore and less conspicuous forms. The most outstanding feature of the island-like portion of the levee visited was the seasonal profusion of *Mertensia virginica*. Other outstanding herbs included: *Dentaria laciniata, Viola papilionacea, V. pensyl-*

vanica, Claytonia virginica, Erythronium americanum, Alliaria officinalis, Ranunculus abortivus, Phlox diverticatus.

The dynamics of flood plain formation and its destruction as seen in the erosion patterns and in the vegetation was examined. The trip included a pleasant one-mile walk upstream along the bank of the river with stops to investigate an island, oxbow lakes, old meander patterns, and other features of the flood plain. The diversity of vegetation and the abundance of flowering plants were the outstanding features of the trip. Attendance 15. Leader, Warren A. Wistendahl.

May 15. Tannersville, Pa. bog. Several Club trips have been made to the bog in the past but all were later in the season. The objective of the present trip was to see the boreal bog plants in flower and the date proved to be ideal for the following: *Picea mariana, Andromeda glaucophylla, Arisaema Stewardsonii, Calla palustris, Carex limosa, Coptis trifolia, Eriophorum spissum, Gaylussacia baccata, Kalmia polifolia, Maianthemum canadense, Menyanthes trifoliata, Nemopanthus mucronata, Panax trifolium, Pedicularis canadensis, Polygala paucifolina, Pyrus melanocarpa, Rhododendron canadense, Saxifraga pennsylvanica, Stellaria uliginosa, Trientalis americana* (*T. borealis* in Grays 8th), *Vaccinium atrococcum, V. corymbosum, Viola conspersa, V. cucullata,* and *V. pallens.*

The bog, which is an irregular area about 3 miles long and ⅛ to ¾ mile wide, lies along Cranberry Creek and is rich in uncommon plant, bird, and animal life. A movement is under way by the Conservation and Garden Clubs of Monroe County, Pa. to purchase the bog for a nature sanctuary. Last winter a number of black spruces were cut in the bog and sold for Christmas trees, though this is a poor species for that purpose. Some large white pines and hemlocks were taken for lumber. The Daily Record, of Stroudsburg–East Stroudsburg, Pa., has published articles on the bog and the efforts of conservation groups to save it.

A fine display of *Rhodora* and painted trillium was seen on Route 196 a short distance north of Mt. Pocono. Attendance 15. Leader, Louis E. Hand.

May 28. Marine Park Beach, Staten Island. Shore birds were not very much in evidence as the tide was high and the usual feeding ground for these birds was under water. A small flock of ruddy turnstones and black-bellied plovers were observed at close range. A mother killdeer was pulling her broken wing act to draw the attention of the observers from her chick which was running into the weeds. A small stand of *Hudsonia tomentosa* was seen in flower. The last remaining stand of *Clematis ochroleuca* on the Island was very lovely to see in full bloom. Attendance 14. Leader, Mathilde P. Weingartner.

June 5. Cheesequake State Park, Middlesex County, N. J. Although this date was picked to find stemless lady's slipper in bloom we were too late for that. Several plants were seen. It was the height of anthesis for mountain laurel and some 20 other species of less massive effect. Many had not seen persimmon in flower previously. Four species new to the park list were *Asclepias variegata, Carex vestita, Hypochoeris radicata,* and *Isotria verticillata* (*Pogonia*). Another new record was the mud turtle (*Kinosternum subrubrum*). In assessing the effect of the Garden State Parkway, we found it adding few if any people to the Park. Shoulders and drainage are not stabilized and there is much erosion. Some new lagoons have resulted and one was coming up thickly with *Sagittaria.* In addition to picnic area and woodland demolished we regret the loss of some excellent stands of mountain laurel, trailing arbutus, hundreds of stemless lady's slippers, and the unique little bog. Attendance 18. Leaders, Dave Fairbrothers, John Small, and Warren Wistendahl.

BOOK REVIEWS

Soil Fertility. By C. E. Millar. 436 pages, 116 tables, 53 figs. John Wiley & Sons, 1955. $6.75.

C. E. Millar has presented a highly important and valuable volume dealing with soil fertility. Literature on this subject is voluminous and in many cases there is some lack of unanimity of concepts. The author, however, with his years of rich experience as a

scholar, teacher, and investigator, has carefully drawn together and presented well the concepts of soil fertility. American literature has been carefully reviewed, and the book emerges as a clear, concise treatment on the subject. Workers in biological and some of those associated with the physical sciences cannot help but gain much information from this volume. If the reader has some knowledge of soils, chemistry, physiology, and farm crops, he will be able to follow the treatment with ease. Without a working knowledge of these sciences, the average reader can still gain much valuable information.

There are 19 chapters in the book. The first chapters take into consideration plant growth, the soil solution, colloids, soil reaction, and related subjects. This is followed by a good discussion on the role of the elements essential to plant growth. Micro nutrients are discussed briefly. The latter portion of the book deals with soil deficiencies, soil organisms and finally a discussion of manures, fertilizer application and crop rotations. The chapters are arranged in an orderly manner for effective subject treatment.

There is little to be said concerning the book which would not be complimentary. There are several items of a minor nature which could have been omitted without losing the effectiveness of the book. For example, the reviewer's opinion is that the clay crystal diagrams on pages 54–55, on the basis of information presented, will have little meaning to the average student of soil fertility and soil management. There are broad sweeping statements on genesis and distribution of clay minerals which would be open for further discussion. For example, on page 56 the author states that the ferro-magnesium silicates of basic igneous rocks such as basalts, give rise to montmorillonite. Nearly all of the references throughout the book are of American workers. There is a rather striking paucity of reference to the foreign literature and an uninformed reader may get the opinion that all important contributions to soil fertility have been made by American workers. It is true that American workers, especially in more recent years, have produced a great volume of literature, but much of it is a recapitulation of concepts developed earlier in other countries. Either the foreign literature should have been given its just position or else statement should have been made as to the reasons for its omission.

The text is well written and it should stand as an important document for many years. The late Dr. Millar could not have left a more fitting monument to himself than he did in writing this book. It is highly recommended for everyone whose scope of work deals in soil-plant relationships, directly or indirectly.—J. C. F. Tedrow, Department of Soils, Rutgers, The State University of New Jersey.

New Textbooks in Ecology

The publication of three texts in general ecology within the last two years is an encouraging indication of an awakening to the need for understanding of the maze of biological interrelationships which influence the activities of each of us. These texts should facilitate better training in ecological principles for students in fields other than biology as well as for biologists themselves.

The author of any text in ecology is faced with a tremendous problem in deciding those items to include and those to omit. Organization of material becomes critical in a field whose scope is so all inclusive. Each of the authors whose books are reviewed here has approached this problem differently. Dr. Clark has emphasized the environmental factors and the variety of effects they exert on the organism. Dr. Odum has precisely formalized and stated the principles which underlie ecological phenomena and then illustrated these principles. Dr. Woodbury has used a modified environmental approach with emphasis on the biological and historical elements. None of these three men is a botanist and so in each case the emphasis tends to be zoological.

Elements of Ecology. By George L. Clarke. 534 pp. John Wiley & Sons. 1954. $7.50.

Dr. Clarke states that his objectives are to "... bring together in one place and in a simple way, the elements of ecology ..." and "... to stress the unity of ecology and the necessity for including the influence of both plants and animals as well as the physical

forces as part of the environment.'' To accomplish this he discusses the factors of the environment as they are both limiting and stimulating to organisms. In an introductory chapter Dr. Clarke defines his terms and delimits his approach stressing the dynamic nature of ecology and the fact that the ecologist focuses his attention primarily on the interrelationships between the organism and its environment. In the following chapters he begins with the more general and stable factors of the environment and progresses towards those which are frequently modified. The chapter on ''the medium'' for life describes the many different ways in which the surrounding medium may influence the development of the organism. The next chapter discusses the substrate on which life exists and rests —as distinguished from the medium. This distinction is a useful and rather novel one. The chapter on substrate concludes with a brief discussion of soils. Chapters on water, temperature, light, carbon dioxide and oxygen, and nutrients follow in what appears to be a fresh approach to the physical environment.

The contents of the chapter on light are indicative of his method. Here one finds a discussion of the sources and distribution of light, light on land and in the water, the biological effects of the amount and quality of light on activity, vision, orientation, periodicity, lunar periodicity, control of flowering, and migration. This is supplemented with comments on ultra violet light, the effect of light in photosynthesis, and shade tolerance. Altogether this is a wide ranging discussion which presents a great amount of information.

Dr. Clarke's specialty and inclinations are obvious throughout. His illustrations are drawn extensively, though not exclusively, from the fields of Limnology and Oceanography. This adds interest equally for the landlocked middlewesterner or the urbane dweller in a coastal city.

The biotic aspect is developed by discussing first the relationships within species and then among species. Dr. Clarke then considers the community, which he defines as ''. . . a group of mutually adjusted plants and animals inhabiting a natural area. . . .'' He goes on to say that ''. . . the recognition of specific communities and their limits is difficult. Part of the difficulty is due to the fact that the community concept has both a functional and a descriptive aspect.'' Dr. Clarke then considers succession and fluctuation in, and the dynamics and productivity of, the ecosystem and concludes with a discussion of the efficiency of the community. Eighteen pages of references follow.

Dr. Clarke writes accurately and interestingly and for those who prefer the environmental approach to ecology this is a highly useful book. With the current interest in the sea it should serve as an excellent vehicle from which the student may obtain an understanding of that complex environment. However, one has the feeling throughout that the problems of the land environment have been somewhat overshadowed by those of the ocean. Dr. Clarke has no specific chapter on ecology in relation to man, but man and his influence are discussed throughout the book.

Fundamentals of Ecology. By Eugene P. Odum. 384 pp. W. B. Saunders Co., Philadelphia. 1953. $6.50.

Dr. Odum has chosen to clarify the complex inter-relationships of organisms and environments by elucidating a series of basic principles and concepts. Each concept is stated briefly, next explained and finally illustrated with examples. Dr. Odum's interest in bird populations has led him to use many examples drawn from this field. However, the range of the illustrative material is impressive, including such diverse organisms as flour beetles, diatoms, barn owls, trilliums and man.

The first of the three sections of Dr. Odum's book is concerned with the principles and concepts of ecology. These have been organized into two related groups of chapters.

The delimitation of ecology as a science is followed by a consideration of the concepts of ecosystem, habitat, the ecological niche and biogeochemical cycles. A discussion of limiting factors is reinforced by an extensive listing of the physical components of the environment. Energy in ecological systems is considered in a stimulating chapter which begins with a review of the laws of thermodynamics and ends with a discussion of

productivity. This chapter features useful examples of energy relationships including an alfalfa-calf-boy food chain.

Following an introduction to population and community concepts, a chapter is devoted to the relationships within populations of a single species. Considered here are all aspects of species development, birth rate, age distribution, density, etc. The reviewer regrets that here as elsewhere few of the illustrations are chosen from plant populations. The next chapter on organization at the interspecies level leads to the principles of species interaction. The final group of concepts are those involving the whole biotic community, including ideas of succession, climax and ecotone.

Three chapters dealing with habitats and their related ecosystems comprise the second part of the book. Odum follows a discussion of the fresh water environment with one on salt water as a medium and finally considers terrestrial habitats, mentioning briefly the major biomes.

The last section of the book consists of three short chapters, on applied ecology, natural resources, public health and welfare and human society. While these chapters provide stimulating reading, one could only wish that the wealth of material presented were not so carefully condensed.

Dr. Odum gives us frequent glimpses of the close relationship between physiological processes and ecological phenomena. The correlation and fusion of such data from related disciplines, especially physiology and genetics, is essential to future progress in ecology.

Odum's treatment of different subjects is not entirely uniform. There is only a brief discussion of the major biomes while the consideration of the concepts of organization at the species population level is extensive. However, the reader will find that ample material is available on biomes while the concepts of species ecology and interaction are in need of this clarification.

For the teacher and conservationist Odum's book is a source of much valuable information. More important, however, he has made a major contribution to organized thinking in ecology. This lucid approach will help to provide the sound basis necessary to explore the intricate problems implied in his closing sentence "... diligent study of man and nature (as a unit, not separately) is in order before we can even begin to entertain the idea that we are masters of our destiny."

Principles of General Ecology. By Angus Woodbury. 503 pp. The Blakiston Co., Philadelphia. 1954. $6.00.

Dr. Woodbury follows his introduction with a chapter on the historical perspective in ecology; a worthwhile feature not found in either of the other texts. Next he discusses organisms and environment in a general way and here again he places the modern plant and animal in their proper positions in respect to past development. Throughout his book Dr. Woodbury reminds us that the organism today is the result of eons of progress and change under the influence of all of the ecological factors. Perhaps this approach is encouraged by Dr. Woodbury's own environment. The evidence of past ages, exposed in the bare faces of the massive fault blocks of the Wasatch mountains, is inescapable. Time as a function and factor of the environment is felt far more directly in his book than in the others.

Dr. Woodbury discusses the physical environment of plants in several chapters, the first of which is fairly typical. It considers briefly the history of the earth and the continents. This is followed by a discussion of orogenic cycles, sedimentation and the development of relief. Soils are considered both as to development and to structure after which the relationship of soil to water, soil classification and soil biology are summarized. In the following chapters, water, air, radiant energy, climate and adaptations to meet the physical environment are all covered in a similar fashion.

The treatment of biotic interrelationships, which occupies the greater part of the book, begins with a chapter on biotic communities and is chiefly devoted to defining and elucidating the nature and methods of classifying communities. The development of communities is handled in a rather brief chapter in which reference is made again to geologic

succession and the impact of time. The following chapters consider community analysis, conditions of existence, food relations, reproduction and population problems. Information is presented in other chapters on cycles, dispersal and evolution, biotic rhythms and migrations, biotic adaptions, historical distribution, geographic distribution, consortism, social relations (both aggregations and societies primarily of animals) and finally ecology and human affairs. His book ends with a 24-page bibliography which contains many references on historical ecology and geology. These are worth reading by the ecologist who desires a broader understanding of the phenomena with which he deals than that which he gets from his biological training alone.

Dr. Woodbury has amassed a great deal of information, not all strictly ecological but on the other hand very useful, although some of it seems extraneous in an ecology text.

The reader has already noted that despite the synonomy in title, "Elements of Ecology," "Fundamentals of Ecology" and "Principles of General Ecology" are in actuality three quite different books, each reflecting its author's personality and interests.

Odum's presentation in "Elements of Ecology" is the least traditional of the three, and is the least replete with facts. Necessarily, there is some overgeneralization. The book, however, is one which should make possible the presentation of the fundamentals of ecology in a form both organized and clean cut. Generalizations are necessary if a science is to be readily comprehended and sold to as critical and demanding a public as the university student. As a text, Odum is suitable for a one semester course and could be supplemented readily for a year's course.

In "Fundamentals of Ecology," Clarke uses a more familiar and traditional type of presentation, and in so doing does not emphasize principles as such so clearly. However, his chapter organization is done in a highly successful and definitive manner and concentrates attention on the factor being discussed. For those who prefer that a text include considerable factual data and especially for those who teach in an area where aquatic habitats are familiar and important, this book would "fill the bill."

If one has a definite predilection for teaching ecology in conjunction with evolution, Woodbury's "Principles of Ecology" is a suitable text. There is a great deal of information contained in this book, albeit some is of a basic rather than ecological nature. The format of the book is on the whole not as clean cut as that of the other two. The chief weakness, as another reviewer (Bendell) has suggested, ". . . is the lack of any critical discussion of concepts which might stimulate the reader to independent thought." Nonetheless, if it is not used as a text, there is ample value herein to make this book a very worthwhile addition to the reference shelf.

There are, in all three of these books, a few minor errors and misconceptions as well as habits of writing which may irritate one or another reader. Nonetheless, the publication of each of these texts will further the development of ecology as a science. For other opinions on these books, the reader may consult the following reviews:

On "Fundamentals of Ecology":

A New Ecology Text Book. By Edwin Moul. Ecology **35**: 297, April 1954.

Ecology—An Initiation. By Peter Frank. Ecology **35**: 297, April 1954.

Fundamentals of Ecology. By Forest Stearns. The Garden Journal **4**: 161, September 1954.

"Elements of Ecology." By L. C. Birch. Ecology **36**: 368, April 1955.

"Principles of General Ecology." By J. F. Bendell. Ecology **35**: 585–587, Oct. 1954.—FOREST STEARNS, Dept. of Botany and Plant Pathology, Purdue University.

Handbuch der Pflanzenkrankheiten. Vol. 1 Die Virus- und Bakterienkrankheiten. Part 1: Viruskrankheiten. E. Köhler and M. Klinkowski. O. Appel and H. Richter, Eds. Paul Parey, Berlin, ed. 6, 784 pp. illus. 1954. DM 150.

Sixty-six years ago, when the first edition of Paul Sorauer's textbook of plant diseases appeared, 250 pages covered the whole field of plant pathology. The growing knowledge of plant diseases has been reflected in the several consecutive editions of Sorauer's

handbook that have appeared since 1888. The present, sixth edition, is expected to require fifteen volumes, of which the above-mentioned part dealing with virus diseases has 784 pages.

The introduction comprises 132 pages of general information written by E. Köhler. It deals with infection, symptomatology, virus inactivation and inhibition, ways and means of transmission, diagnostic principles, interference in mixed infections, host range, susceptibility, and control measures. This part is perhaps too condensed as compared to the second section (573 pages) which is concerned with the particular diseases. In organization the second section follows a sequence that is very familiar to plant taxonomists. Specific diseases are arranged by orders of host plants according to the Engler and Prantl classification, starting with viroses of the Gramineae and finishing with those of the Compositae. Diseases of the Chenopodiaceae and Solanaceae are discussed by Köhler, while Klinkowski covers the cultivated plants of the remaining families. Whenever known, the historical background, distribution, symptomatology, host range, means of spreading, vectors, physical and chemical properties of the viruses, their relationships and means of prevention and cure of particular diseases are indicated. This well written and attractively illustrated manual is valuable because it presents an extensive treatment of almost all plant virus diseases known today, with detailed accounts seldom equaled elsewhere in the literature. In addition to diseases of economic importance, several others known so far only from laboratory investigations, as for instance wound tumor or clover club leaf, are also discussed. The accuracy and extent of the information is gratifying and references to American literature are up-to-date. At the end of each detailed description of a disease there is a bibliography of world-wide publications prepared in a very thorough manner. These bibliographies are invaluable to investigators because they cover not only the more accessible English, German, French, Dutch, and Italian literature, but also less accessible papers which have appeared in Russian, Japanese, and other languages. At the end of the volume there is a well arranged index by topics. The maintenance of quality in photographs, obtained mainly from the archives of the Berlin-Dahlem collection, shows that special care has been taken to secure original prints and thus to avoid the cumulative fogginess of reproduction which so often mars good textbooks. The numerous illustrations, the type and the paper are excellent. The book is bound in cloth.

It is a difficult matter for the authors of a summary such as this book to regiment the wealth of available detail in an orderly array. Yet this remarkable volume manages to present in a highly informative way the facts and concepts of plant virus diseases. Prepared with painstaking care and thoroughness, this classic handbook ranks as the most authoritative reference work in its field. There are few, if any, important omissions. Each chapter or discussion maintains the same high standard of excellence characteristic of other portions. Those who read German will welcome the appearance of this up-to-date work. No equally comprehensive book has yet appeared in English.

The revised edition also brings up-to-date the available information on virus classification. Binomial nomenclature is used throughout the book together with common names of viruses.

This volume will be consulted time and again by plant pathologists all over the world and will be used as a standard reference. The authors are to be congratulated on compiling and critically sorting such a large amount of data.

There are, naturally, minor points on which the reviewer does not see eye to eye with the authors. These are too few, however, to diminish admiration for this scholarly and stimulating book. Undoubtedly it will find its way to all plant pathology and botany libraries. Most individual workers will find its cost too high (DM 150 equals ca. $37.50), but the high price of the book probably could not have been avoided in view of the exhaustive literature citations and numerous illustrations. The book can be recommended as a valuable source of information for all who are interested in the virus diseases of cultivated plants, the disease symptoms produced by various viruses, the geographical distribution of the diseases and methods of control. The appearance of this volume is indeed a welcome event, for the fast-growing literature on virus diseases of cultivated plants has made the need for a work of this character greater than ever before.—KARL MARAMOROSCH, The Rockefeller Institute for Medical Research, New York, New York.

Genetics and Human Heredity. By J. Ben Hill and Helen D. Hill. xiv + 526 pages. 202 figs, 53 tables. McGraw-Hill, New York, 1955. $6.50.

It should appear, to many of us teaching in the field, that this is the book which most authors have promised to write "some day." It would be difficult to conceive of a more thorough treatment of genetics short of adding more examples and explaining, in detail, the enzymatic reactions involved in gene action. The five individuals who have assisted in drafting the illustrations have done quite well. Most students should experience very little difficulty in understanding the genetic principle behind each figure.

In almost every instance, the topics covered are clearly explained and amply presented with sufficient follow-up, as in a lecture, to ensure a fairly adequate understanding. Should this fail, the figures should indeed clarify the point.

Such topics as mitosis and meiosis, Mendalism, linkage, sex-linkage, duplicate genes, aneuploidy—euploidy and chromosomal aberrations, and gene action in development of heritable traits are exceptionally well treated.

Chapter 15, "The Statistical Consideration of Quantitative Characters in Living Organisms," and Chapter 16, "Population Genetics," constitute a short course in biometrics. Any beginner in genetic research would do well to read these 43 pages several times for the simple, elementary, but basic information.

A summary found at the end of each of several chapters is very stimulating to the student who plans to embark upon answering the questions and problems which follow. The "Data" or leading paragraphs of information pertinent to the questions which follow is something new to me. In it is assembled just about all the information the average student needs to know before answering the questions.

The four chapters on human heredity are excellent. They give the student the essential knowledge to which he may quickly add other related conditions. There are references to human conditions (anomalies and diseases) in other chapters as well.

Throughout—besides being an informative and well-written book—it is quite obvious that the authors have had years of experience in the field. The most probable explanation for certain conditions is expressed in good, sound scientific terms. The use of enzymological, serological, and medical terms are not loose or broad but quite accurate.

With the proper selection of materials, it should be possible to use this book for a one-semester course, preferably after a course in elementary physiology. Whether it be a continuation in the field of botany or zoology, the book should score well. It would be difficult to improve on without writing an encyclopedia.—R. J. DEFALCO, Rutgers, The State University of New Jersey.

The Botanical Lore of the California Indians. By John Bruno Romero. viii + 82 pages. Vantage Press. New York. 1954. $2.50.

Over 120 species are discussed, largely plants of reputed medicinal use. There is also a list of edible fruits and a reference to basket making. No attempt is made to produce a formulary or materia medica but ailments ranging from anemia to wounds come under the author's purview. Many of the species named are present in the east or represented there by a similar form.

We found poison oak roots properly dried and made into a tea to effect immunity but the author notes: "I ask my readers not to try this serum pending further laboratory experiments."

There are directions for cremation and burial. Catching fish by intoxicating them is explained. Wild garlic pulp may be used to ward off rattlesnakes. A juice from the bark of red oak "is a very efficient means for straightening and setting loose teeth."

The Indians apparently caught up with new plants rapidly because a quick check showed the following introduced plants in the book: *Achillea millefolium*, *Anthemis nobilis*, *Malva rotundifolia*, and *Plantago major*. The author is at variance with some of the manuals in stating that *Achillea millefolium* "is indigenous to the midcoastal range woodlands." The ecologist, or householder, will know *Plantago major* from a wider range than is implied by "Its habitat is swamps and localities where there is abundant mois-

ture.'' May one wonder if Vantage Press had the manuscripts checked by a botanist or by a pharmacologist?—JOHN A. SMALL.

Hawthorns of Wisconsin. By Emil P. Kruschke. 124 pages, 57 figs., bibliography. Milwaukee Public Museum. $2.50.

This is No. 2 of the Milwaukee Public Museum Publications in Botany and Part I of the above title. This part has the sub-title, ''Status, Objectives, and Methods of Collecting and Preparing Specimens.'' It is stated that Part II, ''The Classification and Distribution of Hawthorns in Wisconsin,'' will be published shortly hereafter.

A section titled ''The Status of Hawthorns Generally'' enlightens the reader about the confusion which leads so many of us to avoid the genus. Wisconsin too has had its problems with *Crataegus*. It seems likely to the author that the number of species will ultimately be nearer to 200 than to the high mark of 1200 once attained. Sometimes 30 to 40 species are reduced to a single species upon restudy. *Crataegus macrosperma, C. pruinosa,* and *C. succulenta* var. *macracantha* appear to be the most rugged survivors in engulfing the formerly separate entities.

This part states the problem that was set up 13 years ago, describes the field-collecting program, collecting equipment and methods, taking data, pressing, mounting, labeling, and filing of specimens. Each of these steps has been meticulously worked out. Descriptions of the steps are full and often beautifully illustrated. You could not find a better manual of collecting and mounting techniques. But after reading this one you might decide to abandon the whole project. If so, it might be just as well because a useless herbarium sheet takes just as much room as a dependable one and may lead to the confusion that has plagued *Crataegus* for so long. We anticipate the publication of Part II and we hope to find an appropriate reviewer for it.—JOHN A. SMALL.

Winter Key to Woody Plants. By Arthur Harmount Graves. 33 pages. Published by the author, Wallingford, Conn. 1955. $1.35.

This brochure is designed for use with ''Illustrated Guide to Trees and Shrubs'' by the same author (1952. $4.00) and to progress beyond the genus it will usually be necessary to have this or another manual. In any event this is a worthwhile supplement, but. being 25 pages of just keys, the value of having the Illustrated Guide to which page reference is made will be readily apparent.

Like most keys, this one works best if you know the plant that is being keyed. Authors always know the plants to which they are making keys. Using the key therefore becomes a sort of mind reading job. Authors sometimes have difficulty in making up their minds and the user encounters that mental-telepathic road block ''lvs. more or less parallel-veined.'' etc.

The multiple choice key is not always consistent. You choose between 1 and 1, 2 and 2, etc., but under Angiosperms you find ''A. Buds opposite or whorled. Lvs. *evergreen*'' and looking for ''A'' again you find ''B. Buds opposite or whorled. Lvs. *deciduous*'' then 5 pages later ''C. Buds alternate. Lvs. *evergreen*'' and on next page ''D. Buds alternate. Lvs. *deciduous.*'' These are major decisions, ordinarily easy to make. They should stand out more prominently by use of boldface type, cross reference, or some other device.

Trying the key on a Torrey trip, most of our trouble came with the largest group, ''D'' above. On page 14, one has a choice among 17 possibilities, intended to make, shall we say, a polyfurcating key. Accustomed to decide between vines and not vines, it became confusing to decide between vines and ''stems with thorns, prickles or bristles,'' and 15 other possibilities which might apply to vines as well as not vines. However, these choices are the same as in other keys and if you are careful to interpolate the negative choice after each positive statement and be sure that it applies before going on this summary will be helpful. In fact you can move all the way from choice 6 to choice 120 on the one page with these 17 decisions. When one becomes adept in using this summary it will make keying much easier and much more rapid.

On page 14, under Angiosperms, four genera of Gymnosperms are keyed. Being

deciduous genera, this is perhaps a commendable aid in locating these genera during the winter months. It was surprising however to find *Ginkgo* had been omitted in the earlier section of Gymnosperms. The choice between "True terminal bud present" and "True terminal bud absent" will be impossible for many customers of this key. Checking with *Ulmus* and *Tilia*, I wonder how the user is expected to know that the buds on the ends of the branches are not truly terminal? To be sure, this choice is the last resort but it does involve 20 genera.—JOHN A. SMALL.

Laboratory Exercises on the Plant Kingdom. By Paul C. Lemon and Norman H. Russell. viii + 121 pages. Wm. C. Brown Company, Dubuque, Iowa. 1954. $2.50.

This spirally bound manual is of the work-sheet type with a minimum of repetition from the textbook and a maximum of thought provoking questions, prepared drawings to be labeled, and spaces for original sketches. Each exercise is followed by a list of "Selected References" which are indeed selected for the student wishing further elementary material or the student ready for the advanced treatises. As a general thing R. D. Gibbs' "General Botany" (Blakiston 1950) is among the references. This is understandable in view of the sequential similarity of the two books. Reference is made to several of the other elementary botany textbooks where they are particularly appropriate.

Thirty-six exercises are included. It is my belief that if the indicated materials and references were available a student could work these exercises with a maximum of independence. It would be an interesting experience. It must be kept in mind however that the manual covers only the reproduction and systemics of plants, including families of monocots and dicots and a winter key to trees. There is neither morphology nor physiology. Two exercises in plant ecology terminate the series.—JOHN A. SMALL, Douglass College, Rutgers, The State University of New Jersey.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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